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THE
AMERICAN NATURALIST

VOL. LIX

January-February, 1925

No. 660



CONTEMPORANEOUS ORGANIC DIFFERENTIA-
TION IN THE SPECIES OF PARTULA LIVING
IN MOOREA, SOCIETY ISLANDS

PROFESSOR HENRY EDWARD CRAMPTON

COLUMBIA UNIVERSITY

INTRODUCTION

THE present communication records some of the results obtained in the course of an intensive investigation of certain land-gasteropods that live in Moorea. It has been found that many species of the animals in question give trustworthy evidence to the effect that the processes of varietal differentiation have gone forward in recent decades and are still continuing with truly remarkable rapidity. While the degree to which real diversities have been brought about does not amount to that of specific distinction, yet the differences actually demonstrated are exactly the same in nature as those by which true species are distinguished. Because much time is still required for further field-work and for the necessary biometric analysis of the material now in hand—amounting as this does to more than forty-five thousand specimens—it is deemed wise to offer now a general statement of the outstanding qualitative results which will indicate the character of the investigation and the nature of its present conclusions.

Since 1906 the writer has been engaged in a study of the variation, distribution and evolutionary relationships of the species belonging to the genus *Partula*, which occur

in islands of the Pacific Ocean under conditions that are exceptionally favorable for such investigations, for by virtue of their insular situations, their degrees of geographical isolation or proximity are defined with absolute clearness. In general, each group of islands bears species which occur in no other group; there is one known exception which only serves to emphasize the observed rule. Within the confines of a given group the several islands bear their own distinctive forms, again with rare exceptions. Finally, the several valleys of one and the same island constitute the homes of colonies which, in correlation with their nearer situations, are more alike than are any two associations living in separated islands; yet they differ more or less as regards the particular combination of the characteristic island species or with respect to the particular varieties of such species as are represented in them.

My interest in these snails grew out of a desire to study a series of related forms in their natural settings, in an effort to determine the relative values of congenital and "environmental" factors of organic structure. At first it was planned to employ the methods of biometry and genetics in an investigation of the Achatinellidae of the Hawaiian Islands, which served Gulick for his classic studies; but the advice of Mayor and Cooke turned my attention to the Partulæ of the Society Islands instead. Mayor had published a brilliant and suggestive paper (Mem. Mus. Comp. Zool. XXVI, No. 2, 1902) on certain species which he had collected in six valleys of Tahiti, where he found the same conditions existing as among the Hawaiian Achatinellidae; therefore it seemed probable that a more thorough and comprehensive study of the species of *Partula* from the valleys of the inhabited islands would yield profitable results.

Another circumstance of the greatest importance was that the noted naturalist, Andrew Garrett, has devoted years of his life to the collection and study of shells throughout many regions of the Pacific Ocean and else-

where. He gave particular attention to the genus *Partula*, and his writings include an extensive and detailed account of the Society Island forms, whose characters and geographical locations he described with extraordinary thoroughness. (Proc. Acad. Nat. Sci. Phila., Vol. IX, Part 1, 1884.) In addition he supplemented his verbal descriptions by a series of outline maps in which he gave the exact localities and ranges of all the Society Island species and major varieties, as these existed during the years of his explorations, 1861-1888. The maps in question were published by Hartman (Bul. Mus. Comp. Zool., Vol. IX, No. 5, 1881); and while they are inaccurate in certain details of outline and proportion, owing to the lack of suitable charts in Garrett's time, nevertheless they are valuable additions to the lengthy publication cited.

Personal explorations in seven different years have been made in several of the insular groups throughout Oceania, but particular attention has been given to the Society Islands—of which Tahiti is the largest and best-known member—because more than half of the hundred and more species of the genus are inhabitants of this one group. During four field trips from 1906 to 1909 inclusive, the islands of Tahiti, Raiatea and Tahaa were completely explored and their species were collected in satisfactory abundance, while Huahine and Borabora were partly worked over. Moorea, which lies about twenty miles to the west northwest of Tahiti, was only partially surveyed in 1907 and 1909, and a return journey was undertaken in 1919 for the purpose of completing the field work of this island. At the later date, however, new collections were obtained in a few of the valleys which were investigated during the earlier years, with the surprising discovery that changes in the constitutional characters of some of the colonies seemed to have taken place even in the few years that had elapsed. Consequently, in the summer of 1923 an almost complete resurvey of Moorea was made, when more than 30,000 specimens were

collected from over 60 localities; when this wealth of material was closely examined and compared with the former collections, it afforded ample evidence that varietal differentiation had actually taken place in numerous ways and among several species, not only during the longer interval from Garrett's time to my earliest work, but also in the course of the short period that had passed since 1909.

The results of the researches in Tahiti have been published (Carnegie Inst. Pub. No. 228, 1917), and a volume on the species of the Mariana Islands is now in press. The first publication is fundamental in more senses than one in its statement of the nature and purposes of the whole series of researches upon *Partula* and in its record of the conclusions which have been drawn from the qualitative and quantitative study of the species dwelling in Tahiti. Only a few of the results need to be restated here, on account of their significance in relation to the discoveries in Moorea. *Partula otaheitana* occurs everywhere in Tahiti in one or more of its primary varietal forms. There have been some areal changes since Garrett's time, but these are less important than the constitutional departures displayed by certain colonies and by occasional individuals in some of the localities. Color types unknown to Garrett have been discovered, as well as mutant "giants" and mutant "dwarfs." Sporadic dextral examples were found among sinistral varieties like *P. otaheitana sinistrosa* and *P. otaheitana sinistralis*, and, conversely, reversed individuals were found in colonies composed solely of dextral snails in Garrett's experience. *Partula clara* also exhibited changes which were even more marked than in the foregoing series. It was "very rare" in Garrett's time, and lived only in a restricted area in the southern sector of the island; by 1909 it had expanded its range so as to cover about four fifths of Tahiti, and concurrently its colonies both in the older and in the newer territory had become so differentiated in the qualities of size, shape and coloration that no less than

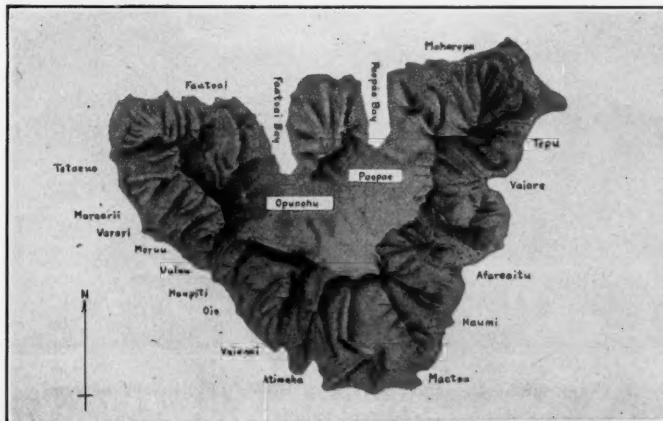
seven primary varieties were distinguishable. *Partula nodosa* also had changed since its first discovery by Garrett, in geographical range and in constitutional respects. These are but a few of the facts which demonstrate the reality of organic differentiation among the Tahitian species, when their later conditions are compared with what they were when Garrett observed and described them.

MOOREA AND ITS ENDEMIC SPECIES

The geographical situation of Moorea is sufficiently indicated by describing it as a near neighbor of Tahiti. It is nearly an equilateral triangle in outline, with one straight side facing north and trending nearly east and west (Plate 1).

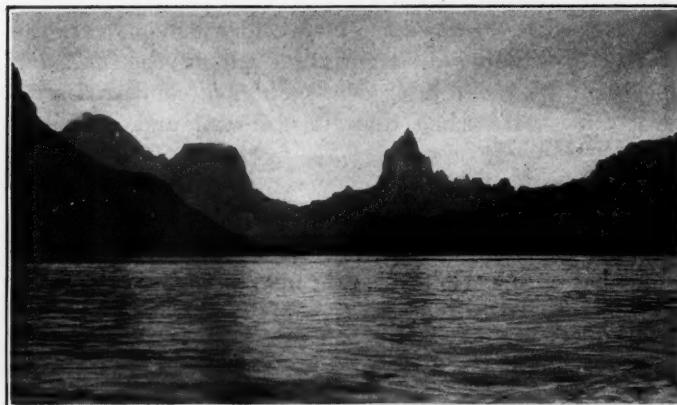
The greatest breadth from east to west is about nine miles, and the axis from north to south is between six and seven miles. The two bays of Faatoai or Opunohu and Paopao indent the northern side; these are clearly interpretable as "drowned valleys," and are features of the

PLATE 1

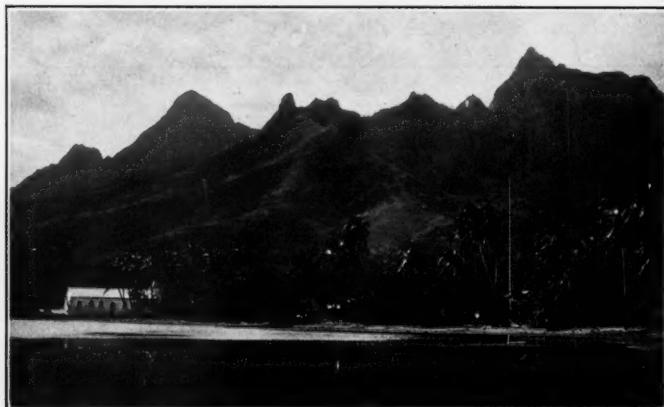


Topography and geography of Moorea, from the official French chart.

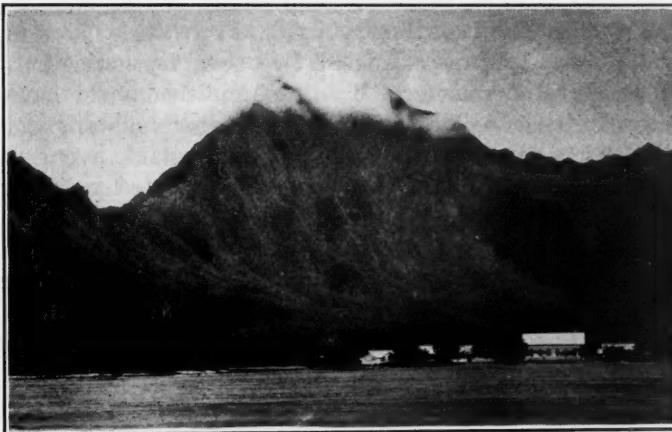
PLATE 2



A. Looking south into Opunohu Bay; from left to right (east to west) the mountains in profile are Tohivea, Tamarutafa, Mouaroa and Mouapu.



B. The region of Haapiti, showing a drier coastal barrier between forested valleys.

PLATE 2 (*continued*)

C. The wide valley of Afareaitu, dominated by Mt. Tohivea, over 4,000 feet in height.

island among many which strongly support the view that Moorea was formerly connected with Tahiti and the other islands of the group, from which it has become separated by subsidence. The major structural feature of the island is a huge amphitheater of lofty mountains that were certainly formed as part of a circular wall of an ancient crater (Plates 1 and 2). The highest peaks of this range, from east to west, are Mouaputa, 2,633 feet; Tohivea, 4,040 feet; Tamarutofa, 3,053 feet; Mouaroa, 2,993 feet; Mouapu, 2,547 feet; and Atiati, 2,514 feet. Another prominent portion of the old crater wall is the mass of Mt. Rotui, 2,930 feet high, which stands between the two bays on the northern side; this is now disconnected from the main semicircle of high land, excepting by the lower levels of the central valleys named Opunohu and Paopao. The outer slopes of the great mountain chain descend abruptly to about 1,200 feet above the sea where they become more gradual as they trend toward the coast. The descending buttresses are covered with dryer plants toward their outer ends (Plate 2, B), while the valleys be-

tween bear the luxuriant vegetation which serves as the dwelling-places of the snails now under discussion. As the lower portions of the dryer ridges constitute barriers to the passage of the animals from one valley to another, such migrations as have been accomplished must have traversed the higher levels where greater moisture and denser vegetation provide more or less suitable avenues. Collections have been obtained in 68 separate localities; some of these are large unitary valleys, such as in Afareaitu (Plate 2 C); others are well-circumscribed areas of lesser size, while still others are subordinate divisions of more open territories, such as the wide amphitheater of Opunohu.

We may now pass to the serial consideration of the species of *Partula* that live in Moorea. Garrett enumerated four as follows: *Partula lineata* Lesson, *Partula taeniata* Mörch, *P. elongata* Pease and *P. mooreana* Hartman. Pilsbry's list of four agrees in part: *P. suturalis* Pfeiffer instead of *lineata*, *P. taeniata*, with which *elongata* is combined, *P. mooreana* and *P. erhelii* Mousson. I concur with Pilsbry's view regarding *elongata*, but in my opinion the status of *P. erhelii* is still in doubt. My own work has resulted in the addition of four other species (*Nautilus*, Vol. XXXVII, 1924), namely, *P. mirabilis*, *P. dendroica*, *P. tohiveana* and *P. olympia*. In addition there are certain forms whose position I am not prepared to define without further study, and these may well be passed over in the present review. There are therefore seven species to be taken up: *P. taeniata*, *P. suturalis*, *P. mooreana*, *P. mirabilis*, *P. dendroica*, *P. tohiveana* and *P. olympia*. The first of these exists in the greatest numbers and it possesses the widest range, while the others follow in graduated order to the last two, which occur in small numbers in very restricted localities.

PARTULA TAENIATA, MÖRCH.

Within the present limits it is not possible to deal *in extenso* with the numerous subordinate forms which come

within the definition of this species. The material is very abundant and diversified, and much time has been devoted to its study in the field and in the laboratory; yet there are several problems concerned with centers of origin, lines of dispersal and even actual relationship which demand more work for their satisfactory solution. However, certain important features of distribution and intrinsic nature are very clear, and some of them fall within the scope of the present discussion.

Like *Partula otaheitana* in its own island, *P. taeniata* now spreads throughout all parts of Moorea, and consequently it is to be regarded as a species of long standing which has been permitted by time and circumstances to multiply and to extend its range widely. Again, like the older species elsewhere, its several colonies have become greatly diversified in numerous characteristics and in various degrees which really require the biometric data for their full demonstration. Sometimes the qualitative differences are plainly evident. In the extreme northwestern colony of Pafatu (Tetaeuo) the shells are large and relatively solid, while in the neighboring valleys from Maraarii to Uufau they are noticeably shorter and stouter. The southern and southwestern associations comprise slender shells which are so thin as to be almost diaphanous; these constitute the primary variety named *elongata*. The northeastern areas are occupied by short, stout and thicker forms, with distinctive features of color as well. The Rotui segment and the Faatoai region bear their own characteristic varieties that are found nowhere else.

While certain color-types have been found which seem to have been unknown to Garrett, and which may perhaps be the product of mutation since his time, no doubt whatever arises with regard to the novelty of *reversed* specimens that have come to light in two widely separated localities. This species has been described as universally dextral, and no shells with the sinistral coil have been collected or noticed heretofore, so far as the literature

and museum series are to be trusted. That ample series of specimens have been observed is proved by Garrett's reference to the "prodigious numbers" and "thousands" of individuals which came under his notice. My own collections of *taeniata* comprise more than twenty-five thousand adults and about an equal number of adolescents and advanced embryonic young, all of which are dextral with two new-found exceptions. In 1923, one dark-colored reversed adult was taken in a small valley near Maraarii, in the northwestern region; it is a typical *taeniata* of its territory. The animal was not gravid, and therefore it can not be known what kind of young it might have produced. Another sinistral individual of this species was also discovered in 1923 in Atimaha Valley—an area of much importance for the study of *P. suturalis* and *P. mooreana*, at the extreme southern end of the island. This specimen was infertile, like that of the northern valley. Both of the reversed snails were full grown, and obviously their origin by mutation must have occurred from one to two years prior to their discovery.

We have in *P. taeniata* a species that has long been dispersed throughout the habitable territories of Moorea, in contrast with others to be described hereinafter. Yet it can not be said to have reached the end of its evolution, for the processes of differentiation by which its varied representatives have come to be organically distinguishable in separated valleys seem to have continued to some extent during the years that have elapsed since Garrett made his fundamental studies. In my own experience with *taeniata*, the most notable discoveries are the two reversed individuals, which can not be anything but products of recent mutation. It is true that the episodes of sinistral transformation are excessively rare; to establish a true variety with the reversed coil would require the coincident origin of several individuals with the novel character, or the direct transmission of the changed body-form to the progeny of the mutant animal. As the case

of *taeniata* now stands, we can not say whether the occurrence of such mutations would be futile, or, if repeated, would lead to the establishment of a new variety or species. Fortunately the data are far more satisfactory in the cases still to be dealt with, in whose terms the history of *taeniata* is in part to be interpreted.

PARTULA SUTURALIS PFEIFFER

The material facts in the case of *Partula suturalis* constitute the most satisfactory body of proof that organic differentiation is a contemporaneous process and that the production of new diverging forms having the status of varieties is the requisite initial phase in the origin from common parentage of more widely separated types that may justly be denoted species. This case is complete on its own evidential merits, and it is still further strengthened by the demonstration of exactly parallel episodes in the histories of other species living in Moorea.

The description given by Garrett definitely portrays the condition of the species and of its varieties for his time, as regards the intrinsic nature of the various colonies and their geographical distribution. My own observations were made at the earlier period of 1907 and 1909, and at the later period of 1919 and 1923. It is therefore possible to compare my earlier observations with those of Garrett and my own later experience with what I had found in 1907 and 1909. When all the data are assembled, they provide convincing proof that the species has spread to an astonishing degree since Garrett's time, that its various colonies have changed in certain definite genetic qualities, that mutations have arisen in various characters such as shape and size and direction of the coil, and finally that mutations are continuing to arise.

Garrett (*loc. cit.*) deals with this species under the name of *P. lineata* Lesson, but in a letter to Hartman he expressed his regret that he used Lesson's name. There is no question as to the shells which Garrett had in mind,

however, and we follow Pilsbry in the use of *P. suturalis* Pfeiffer for this species. Garrett's statements are so important as to demand full and exact quotation, as follows:

This beautiful arboreal species is found in great profusion in Vaianai valley, on the southwest coast of Moorea, where it occurs in company with *P. Mooreana* and *P. elongata*. It also exists in considerable numbers in a small valley about two miles to the westward, associated with *P. taeniata* and *elongata*.

I first discovered this species in 1861 and obtained several hundred specimens, *all* collected on the eastern side of the stream that flows through the valley of Vaianai. They were *all* dextral, and were so described by Pease, under the name of *vexillum*. On a second visit, in 1875, I took over 2,000 examples, *all* gathered on the *western* side of the stream, and was surprised to find many sinistral forms among them. At the same time I found about a dozen specimens, *all* sinistral, in a large semicircular valley on the opposite side of the island. They were probably stragglers from Vaianai.

It is noteworthy that no reversed *Partulae* were found in any other part of the island except on the western side of the stream in Vaianai, and the above-mentioned stragglers taken on the opposite coast. The same side of the stream is also the home of the sinistral *P. Mooreana*.

Several miles to the eastward of Vaianai, in a large valley named Oahumi, it is found equally as abundant as in the former location. The Oahumi shells, which are slightly modified (*= strigosa = alternata*), gradually insinuate with *lineata*. It occurs, also, sparingly in a valley more to the eastward, where it is associated with *P. taeniata* and *striolata*.

These statements are satisfactorily definite as to the geographical facts and also as regards the associates of *suturalis* in the several localities mentioned. Furthermore, they properly distinguish the two primary divisions of the species, denoted *P. suturalis vexillum* and *P. suturalis alternata* in the present article. The name "Vaianai" is still in use for an area which is really a little *west* of the southernmost point of the island, instead of southeast, as Garrett described it and sketched it in the outline map published by Hartman. The valley to the westward, mentioned in the first paragraph of the quotation, is undoubtedly Uufau, which is exactly two miles from Vaianai. The area "on the opposite side" of the island where Garrett's sinistral stragglers were found is Opunohu. The last paragraph refers to *P. suturalis alternata* as occurring in "Oahumi," which should

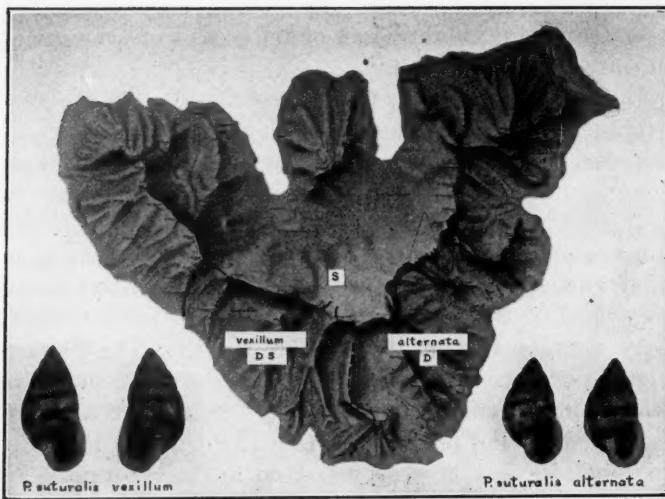
be Haumi, and in the great valley of the Afareaitu region to the eastward of Haumi, which last is clearly specified as the limit in this direction of the extent of the species in Garrett's experience.

But far more important than the matter of mere geographical extent are the data relating to the nature of the local colonies as regards the modes of coiling of their components. The species was fundamentally dextral in 1875, but in Vaianai sinistral individuals existed to the number of fifty out of two thousand, as Garrett states in a later paragraph. None were noted in the valleys to the westward or to the eastward, and surely Garrett would have mentioned them if they had existed. The "stragglers" of sinistral nature which Garrett found in Opunohu are especially noteworthy for future consideration; and in view of the words used by Garrett, it is fair to conclude that he discovered no dextral examples of *suturalis* accompanying them in the Opunohu region. The condition of *P. suturalis* in 1875 is therefore known with substantial definiteness (Plate 3 A).

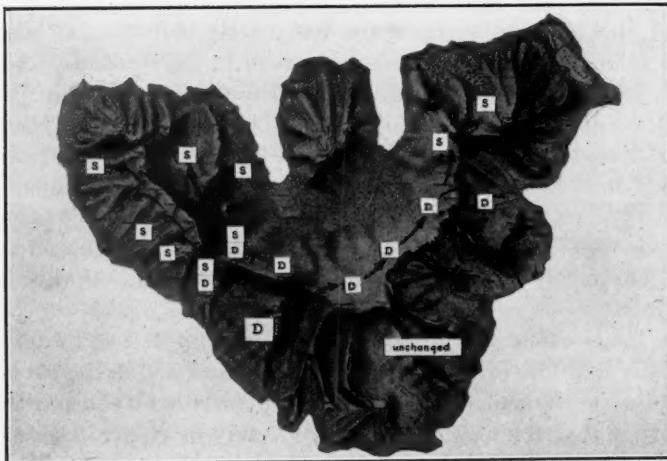
To-day the territorial extent and the intrinsic qualities of the colonies of *suturalis* are vastly different (Plate 3 B). While *P. suturalis alternata* is substantially the same, so far as my present knowledge goes, *P. suturalis vexillum* has spread into almost all of the habitable areas of Moorea, excepting only those of the Rotui sector, which lies between the two great bays of Faatoai and Paopao. And when we pass from the old area of occupation to the new-won territories, the species changes its character from purely *dextral* to exclusively *sinistral* in both directions.

It is beyond the purposes of the present article to deal fully with the evidences so briefly summarized in the foregoing statement, but some of the details are required in order that the nature of the proof may be clear. Beginning with the original valley of Vaianai, we have Garrett's observation of 1875 that two and a half per cent. were sinistral, while in the years of my own work no

PLATE 3



A. The distribution and nature of *Partula suturalis* as described by Garrett.



B. The distribution and nature of *Partula suturalis vexillum* to-day; the arrows show the extent and direction of recent dispersal.

sinistral specimens of *suturalis* have been found in that locality; hence we must conclude that Garrett's reversed specimens were the products of a transitory and sporadic phase of mutation. This conclusion is supported by my own findings in the neighboring valleys of Oio and Haapiti. In the former area, reversed individuals amounting to 1.3 per cent. of the adult population were found in 1919, while in 1923 the sinistral type was absent in the same territory; in Haapiti, about 7.5 per cent. were sinistral in the 1907 collection, but in 1923 not a single snail of this kind was observed.

Passing northwestward, we come to Uufau Valley in which Garrett found no reversed snails at all. In my own collections of 1907, the sinistral component amounted to 87 per cent. of the adult population, while in the series obtained in 1923 this component had dropped to about 71 per cent. of the adult population and to 68 per cent. of the embryonic series. To the northwest beyond Uufau, where the species did not occur in Garrett's time, the valleys are now occupied by *suturalis* in numbers that diminish as we approach the western limit of Tetaeuo, in such a way as to indicate a recent immigration into this sector of the island. Here the species is uniformly *sinistral* with the exception of very rare mutations to dextrality, such as one adult in Moruu Valley and one embryonic snail in the Maraarii collection.

Taking up the colonies of the great amphitheater of Opunohu across the mountains, we must return to the neighborhood of Vaianai Valley, because that area was the center from which the present Opunohu populations must have been derived. This conclusion is inevitable from Garrett's statements that in 1875 sinistral examples were found in Vaianai and Opunohu; the population of Uufau Valley was dextral at that time. Having established themselves across the mountains in Opunohu, the migrants produced descendants which spread to the west, northwest and north, and also to the east and northeast; but the species was prevented by the lack of suitable

avenues of vegetation from crossing the low lands to the median northern sector of Rotui. To-day *suturalis* is *exclusively dextral* in that part of Opunohu which is nearest to the pass from Vaianai, namely, Maramu. To the westward, it is dextral as far as Roroie Valley, near the foot of Mt. Mouapu, but thereafter the colonies are mixed, until with the approach to the Vairahi division of Opunohu Valley the dextral individuals diminish in numbers and appear only as casual mutations among the prevalent sinistral forms, as in Tupuna and Vaiana (not to be confused with Vaianai). Still further north, the species has recrossed the encircling mountains so as to penetrate into Urufara Valley, and, quite independently, into Faatoai Valley, which is the last habitable area in this direction away from the original territory of Vaianai. From my own observations, it is plain that the species is now more abundant in the extreme valleys than it was in the earlier years of 1907 and 1909.

The eastern flood of migration from the first established settlement in Maramu is quite as interesting as the western. All the colonies are now dextral, where the advancing tides of successive generations must first have been sinistral, until we pass Mt. Mouaputa. In the uppermost Paopao region, the species is *sinistral*, and it remains so in the contiguous northern valley of Paraoro, and in the extreme valley of Maharepa; the last-named area has been invaded since 1907. Beyond Mouaputa, *suturalis* has crossed the mountains to the outer circle of valleys of the Vaiare sector, where dextral and sinistral components now exist in company; but in the valleys northeast of Vaiare the former disappear and the colonies comprise only reversed individuals.

In summary, therefore, the most remote colonies at both geographical extremes are found to be alike in their exclusive sinistrality. It seems certain that the sinistral "stragglers" found in Opunohu by Garrett constituted the forefront of a wave of migration which has since spread to the very extremes of the habitable territories.

As they spread more and more widely, the individuals constituting the advance lines retained the sinistral form of coil, but their descendants and their followers returned to the dextral mode as a wave of dextrality swept after. The present lack of reversed snails in Vaianai and Haapiti, where they formerly existed, and the diminished numbers of this kind in 1923 in Uufau, where they constituted 87 per cent. of the population in 1907, are illustrative details among the many which justify such a summary statement of the recent history of *suturalis*.

The biometric analysis of the numerous colonies brings to light other kinds of transformation which are entirely independent of the qualities of spirality. When the standard characters of the shells are defined in terms of their ranges, averages and indices of variation, the several colonies exhibit differences of real significance, which of course have come about as the snails have established their somewhat isolated settlements in places more or less remote from the original territory of Vaianai. Some of the sinistral members of the western Opunohu series are as short as 16 mm, and are therefore no longer than their *taeniata* associates, while some dextral shells on the Opunohu side, not far from the pass leading from Vaianai, attain a length of more than 24 mm. There are also notable diversities in shape as well. Such differences seem to be truly genetic as the colonial statistics indicate. Furthermore, there are types of coloration that are not described by Garrett, and it seems legitimate to interpret these as new mutations from the ancestral modes of fasciation and coloration.

In brief, then, *Partula suturalis* proves to be a species comprising two primary divisions, *vexillum* and *alternata*, which have had very different histories in recent times. The latter has remained substantially the same, hemmed in as it is by relatively impassable barriers of mountain and dry ridge, while the former has changed in several ways and to remarkable degrees during the last few decades. The occupation of larger territory is far less note-

worthy than the alterations in organic nature which are exhibited in spirality, size, proportionate measures and in coloration.

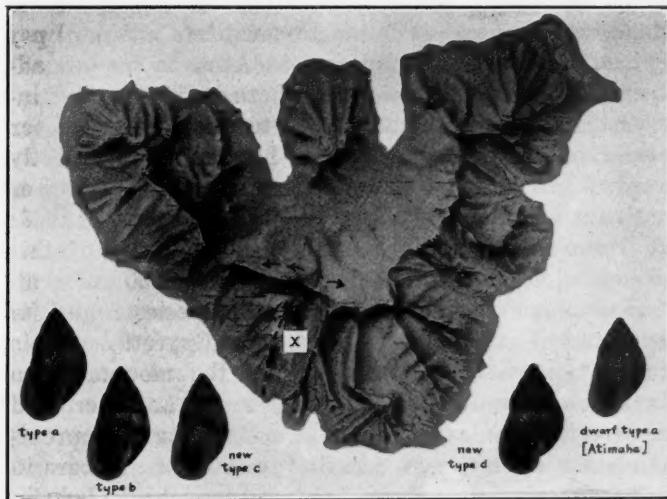
PARTULA MOOREANA, HARTMANN

The history of *P. mooreana* is very much like that of *P. suturalis*; when Garrett explored the island, it existed only in a restricted locality, from which it has since spread, though less widely than *suturalis*. In its original metropolis and in several of the newly occupied regions, it has produced novel mutations of several kinds. It is an interesting coincidence that the former limited habitat of this species was Vaianai Valley, which was also the center from which *P. suturalis vexillum* has now become so widely dispersed.

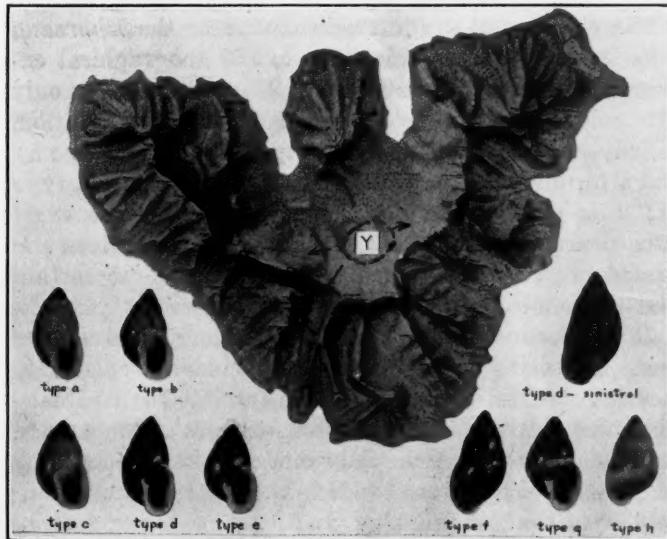
Garrett discovered the first specimens of *P. mooreana* and sent them to Hartmann, who published their description in 1880 (Proc. Acad. Nat. Sci. Phila., 1880, p. 229). In his monograph on the Society Islands species, Garrett gives the following definite statements concerning *mooreana* (pp. 59, 60): "This arboreal species is abundant, and restricted to Vaianai Valley on the southeast coast of Moorea, where it shares the metropolis of *P. vexillum* Pse." "It is *always* sinistral, . . ." "A variety with three narrow pale brown revolving bands is not infrequent." The error in assigning Vaianai to the southeast instead of the southwest coast is a trivial one, already noted (cf. Plate 4 A).

In the course of my own studies, the species was duly found in 1907 in the original locality, from whence large numbers were also taken in subsequent years. In 1909 it was also discovered in the Maramu subdivision of Opunohu, immediately across the mountains from Vaianai; although its relative numbers were few in that year, by 1923 the species had so increased as to constitute nearly 80 per cent. of the Partula fauna in Maramu. Furthermore, it has been taken in valleys on either side of Maramu, its first foothold across the divide from

PLATE 4



A. *Partula mooreana*. X marks the original locality; the arrows show the extent and direction of recent dispersal.



B. *Partula mirabilis*. Y marks the probable original locality.

Vaianai, in areas that extend over a lateral distance of about two miles. Returning to the outer side of the island, the species was found to constitute about 10 per cent. of the Partula population in Atimaha Valley, adjacent to Vaianai on the east, where in 1923 it had increased in relative numbers so as to form almost 80 per cent. Some of the western valleys have also been recently invaded. Oio, next to Vaianai, contained about 15 per cent. of *mooreana* in 1919, and nearly 40 per cent. in 1923; the Haapiti collections of 1907 included none of this species, while those of 1923 comprise about 30 per cent. of *mooreana*. Clearly, therefore, the species began its geographical extension some time after Garrett made his pioneer studies. It spread across the mountains to Maramu and beyond to neighboring areas, and it crossed the eastern boundary of Vaianai to Atimaha at approximately the same time, increasing in relative numbers in both territories; at a somewhat later date it invaded Oio and Haapiti, in which it still exists on the heights from which it has not yet had time to descend to the forested areas of lower altitude.

The changes in the intrinsic nature of the *mooreana* colonies are more significant than the geographical expansion of the species as a whole. Garrett describes only two color-forms in the original Vaianai association, namely, the prevalent unbanded type (Plate 4A, type a) and a form with three pale brown bands (Plate 4A, type b); it is unfortunate that he does not give the exact numerical proportions, but states only that the latter is "infrequent." My own observations make it certain that the banded form has diminished in recent years in Vaianai; whereas the 1907 collection comprised 14 per cent., the series of 1919 and 1923 included respectively only 2.6 and 2.8 per cent. of the fasciated individuals. The same decrease in the relative numbers of the banded type is observed on the Maramu side, where in 1909 nearly 44 per cent. were banded, while in 1919 there were only 8 per cent. of this kind, and less than 2 per cent. in

1923! The Oio, Haapiti and extreme Opunohu colonies furthest from Maramu are composed of the unbanded forms solely. The Atimaha collection comprises about 1.5 per cent. of this three-banded kind.

Other color types have been discovered which are apparently new since Garrett's time. The first is light-colored, with a single narrow median band of brown (Plate 4A, type c). This was *not present* in my own Vaianai collections of 1907 and 1919, but in 1923 three out of 2,000 specimens of all ages were discovered. In Atimaha, 1 per cent. in 1919 and 4 per cent. in 1923 were of this kind. Apparently, therefore, the single banded type is new in point of time, and it seems to be on the increase in Atimaha. Whether the novel coloration has been produced independently in Vaianai and Atimaha or whether it was a product of mutation in Atimaha, whence it was introduced into Vaianai, is a problem which requires additional data for its solution; but the statistical data tend to support the former interpretation.

Another new color type is dark-colored, with a narrow median corneous band, which is therefore the exact converse of the one-banded form (Plate 4A, type d). This was discovered in 1923 in the upper part of Vaianai Valley, *in the same area which had yielded the extensive collections of previous years in which it did not exist*. It occurred in greater numbers than the type with the single stripe.

The next point is one which would not be evident without the biometric analysis of the several colonies; it is the dwarfed size of the shells which form the Atimaha association (Plate 3A, type a Atimaha). The general length of the Vaianai individuals is approximately 17.5 mm, while those of Atimaha center about 15.5 mm; thus the former are about one eighth longer than the latter. It would seem that the first migrants from Vaianai into Atimaha were shorter than the average of their kind, and that they transmitted their abbreviated stature to their descendants of to-day. It is not justifiable to refer the

reduced size to peculiar environmental conditions obtaining in Atimaha, because no such external factors can be discovered and also because the associated species display no parallel diminution in length, as they should if environmental conditions *per se* were responsible for the dwarfed stature of *mooreana* in this locality. The converse of this case is provided by the extreme western colonies of the Opunohu region, where the shells are statistically larger to a degree that is well beyond probable error. Again there are no external circumstances to which the different quality may be referred, and again there are no parallel enlargements to be observed in the accompanying species.

At the last, we come to the most notable mutation as yet discovered in this species, namely, the production of *dextral* individuals. A single right-handed adult was found in 1923 in Maramu, whose affinities with the prevalent sinistral type were indicated by its patent characters of color, size, shape and coloration, while in addition it bore in its brood-pouch *two sinistral young*. Again, in the 1923 collection from Tefeo Valley, adjacent to Maramu on the east, a sinistral *mooreana* was found which contained *two dextral young*. No clearer proof of sporadic dextral mutation could be obtained. The rarity of such an episode may be judged from the occurrence of only these three individuals with direct coil out of a total array comprising well over 9,000 specimens of *mooreana* of all ages.

The words of the concluding paragraph summarizing the observations on *suturalis* might be repeated, so far as they refer to observed changes in the way of territorial expansion, and varietal differentiation; the phenomena are clearly parallel in the recent histories of *mooreana* and *suturalis*.

PARTULA MIRABILIS CRAMPTON

The species now to be considered is the first among several that have come to light for the first time in the

course of the present researches; they have been deemed so noteworthy as to deserve special notice and record (*Nautilus*, Vol. XXXVII, 1924). In view of Garrett's long and careful studies in the Society Islands, it was very surprising to find novel forms which were unknown in the literature and entirely lacking in the extensive collections made by Garrett, sent by him to Hartmann and others, and now deposited in the museums of Honolulu, Washington, Cambridge, Philadelphia and Pittsburgh. I have seen all these collections and it is certain that the new species are not represented in them; it is especially important that they are not contained in the Hartmann collection at Pittsburgh, as Garrett wrote to Hartmann that he (Hartmann) had received specimens of all the forms discovered in Moorea. There can be no question as to the thoroughness of Garrett's explorations, and we must attribute his failure to find the new types to the peculiar circumstances of their distribution in his time.

Partula mirabilis was discovered in 1907 in the Maramu subdivision of Opunohu Valley, and in subsequent years it has been taken in eleven other more or less contiguous localities. About two thousand specimens are in hand. The circumstances under which they exist, and their own qualities are such as to demonstrate exactly the same kind of history which *P. suturalis* and *P. mooreana* have undergone. Apparently the parent colony was so small in the years of Garrett's work as to escape his attention, thus presenting at that period the same restricted condition which we now find in two species later to be described. Like *suturalis* and *mooreana*, but much later in point of time, *mirabilis* began to extend its area of occupation; concurrently it seems to have passed into a period of active mutation, with the result that in the qualities of coloration its colonies exhibit greater differentiation than an equivalent number of associations of any other Moorean species, in an area of equal size. Although the species is predominately dextral, very exceptional sinistral individuals have been found in one circumscribed colony.

The pertinent facts are illustrated in plate 4B. Apparently the original center was somewhere in Opunohu in the neighborhood of Maramu, Tefeo or Irua, whence the tides of migration spread to the west and to the east, and also northward across the lower ground to the southern valleys of the Rotui sector. The 1923 collections from the last-named region comprise far higher relative numbers of *mirabilis* than did those of 1909, hence the northward migration appears to have been accomplished in recent years. Another episode of territorial enlargement is still more proximate in time, namely, the invasion of Vaianai Valley from Maramu; in 1923 this species was found in the upper and middle portions of Vaianai, *from which it was entirely absent* as recently as 1919, when my own collections of all species amounted to thousands of specimens.

The qualitative facts of colonial differentiation may be briefly set forth, without entering into the quantitative details, although the latter are additionally significant on their own merits. The species as a whole comprises at least eight color-types, all of which are shown in Plate 4B: (a) light and uniform in general, with darkened apex; (b) boldly strigated transversely; (c) medium in color with reddish spire; (d) deep brown; (e) with three revolving bands; (f) with a broad revolving zone of deeper color; (g) dark, with a narrow longitudinal band to the left of the median line; (h) dark, with a narrow median corneous band. These are entitled to be called genetic types, inasmuch as they are repeated in offspring, along with young of other kinds whose coincident presence proves that the several color-classes interbreed freely. Each one of the localized associations possesses its own characteristic color composition, marked by the presence of only some of the whole array of color-types and also by particular numerical relations of the component color-classes, which proportions are not duplicated elsewhere. Using the symbol letters for the different kinds, the Maramu colony comprises *c.d.g.* and *f.* types,

stated in their order of numerical abundance, while the association in Faataofe, a small valley to the west, is made up of *d.e.h.* and *a.* individuals. East of Maramu, the *c.e.d.f.* and *g.* types are present. On the southward slopes of Rotui the colonies consist of *c.b.f.* and *g.* individuals only. Finally, the recent migrants into Vaianai are *d.f.* and *e.* forms. From these facts, it may be concluded that the *h.* type is a local mutation in the Faataofe locality, and that the *b.* type has come into existence more to the eastward of the original home of the species. Regarding the *e.* form, it may be that this distinctive pattern has independently arisen in the Faataofe, Irua and Vaianai areas, but it is conceivable that it existed earlier in the central Maramu association, from which it spread into the surrounding valleys where it now persists, while it has disappeared in the locality where it formerly occurred. But whatever may have been the modes by which the various types have originated, the result at the present time is a condition of colonial diversification, entirely similar in principle to what is displayed by *suturalis* and *mooreana*, but greater in degree when the smaller area is taken into account.

Finally, the important observation is recorded that in one of the newly established colonies of *mirabilis* sinistral mutation has occurred. The area is Faataofe Valley, in which three reversed adults were found (Plate 4B, type *d* sinistral); they belonged to the prevalent color-class of dark brown shells. In each of two, a single *dextral* young snail was found, while the third reversed individual contained two *sinistral* young, which therefore perpetuated the transformed character of their parent.

The case of *mirabilis* is very interesting both on its own and on its comparative merits. My personal observations prove its territorial expansion within recent years, and Garrett's failure to record it at all signifies an unusually small area of its occurrence in his time. The history of the species accords with those of *suturalis* and *mooreana* in all essential respects, even to a corre-

spondence in contemporaneous production of novel mutant individuals differing from the generality in the direction of the spiral coil.

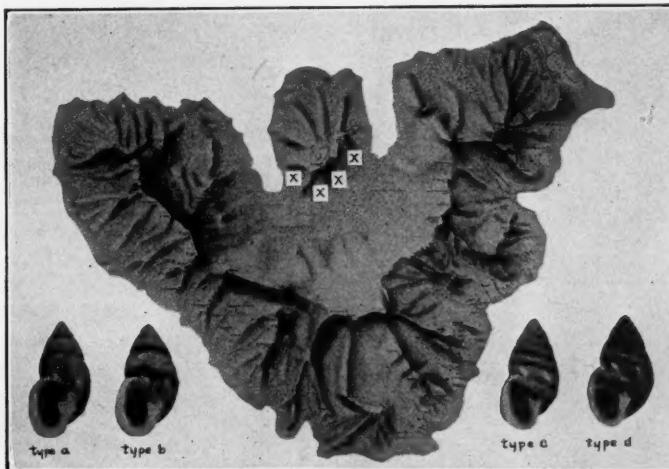
PARTULA DENDROICA CRAMPTON

The second of the newly found forms, *Partula dendroica*, occupies a much smaller territory than any of the foregoing; it therefore presents a condition like that of *mirabilis* not long ago, and of *mooreana* and *suturalis* in more remote decades. It was first discovered in 1909 in Vaihiaia Valley, on the southwestern side of the Rotui sector (Plate 5A), and in subsequent years the species was taken also in valleys on the southern and southeastern aspects of the same mountain mass. The western, southern and eastern slopes of Mt. Rotui are more abrupt than those of the northern seaward side, and their valleys differ correspondingly; thick vegetation grows to an altitude of more than 1,100 feet in the gullies of the southern face, but the heights to which the dense vegetation extends gradually diminish on both sides toward the north. *Partula dendroica* has been found in seven of these subsidiary areas, where it lives upon the trees and shrubs of larger size. The animals are exclusively sinistral.

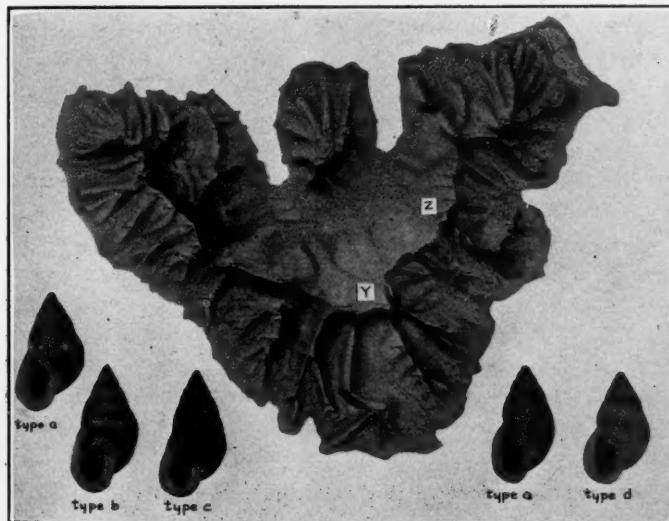
Four color-types are presented as follows (Plate 5A): (a) devoid of bands and with apical darkening; (b) with one median longitudinal band; (c) with four revolving bands; (d) with a broad median zone of dark color. The colonies to the west are composed of types *a.b.* and *c.*, stated in the order of their numerical frequency; the southern colonies differ, sometimes comprising the *d.a.c.* classes and sometimes with the composition *d.c.a.b.* At the southeastern extremity of the whole range only the *a.b.* types are present.

The distribution of *dendroica* suggests that it has recently spread from a more restricted territory which, like that of *mirabilis* some time ago, must have been overlooked by Garrett. The western and eastern borders of

PLATE 5



A. *Partula dendroica*, living in the localities marked X.



B. *Partula tohiveana*, living at the place marked Y.

C. *Partula olympia*, occurring in the region marked Z.

the area now occupied are not marked by barriers to the further extension of the species, whence it would appear that these outer regions have not long been occupied. While there is some degree of intrinsic differentiation of the several valley associations, the differences are far less in degree than those displayed by the *mirabilis* colonies; such considerations also indicate that the peripheral associations have not long been separated from a central parent colony, in which all the principal color-types may be presumed to have been present.

Thus the case of *dendroica* stands next to that of *mirabilis*, as regards the smaller area of occupation, its more recent dispersal and its lesser degree of internal differentiation.

PARTULA TOHIVEANA CRAMPTON

Like the foregoing, *P. tohiveana* is a newly discovered species whose existence in Moorea was entirely unexpected. It was found in 1923 on the high inner slopes of Mt. Tohivea, the dominating mountain of the island (Plate 5B). Several hundred individuals were taken in an area not more than four hundred yards in lateral extent at an altitude of 700 to 900 feet above sea-level. All the animals collected were sinistral.

Despite the small size of the colony, the shells are definitely differentiated in color characteristics (Plate 5B); the three types are (a) plain, (b) encircled with two or sometimes four vaguely-defined bands, and (c) with a broad median zone of color. The distinctions in color pattern are hereditary. The composite nature of the association is noteworthy, for it is here clearly evident that diverse genetic types of color can arise in one and the same compact area of habitation.

This species is significant in certain other connections. It is distinguished from the other sinistral species of Moorea by its general make-up, and by special features such as the roundly dentated lip and simple conical spire. But these very distinctions mark it as a relative of a

group of forms living in Raiatea, an island situated about 120 miles to the west northwest. The latter group comprises *P. callifera*, *P. dentifera* and *P. formosa*, all of which are dextral. If the common characters in question really do signify a community of origin of *tohiveana* and the Raiatea species, then there must have been a prior land-connection between Moorea and Raiatea; upon this larger land-mass the ancestors must have been dextral and sinistral, exactly as *P. otaheitana* and *P. suturalis* now are. With the subsidence of the connecting bridge, the colonies of Moorea and of Raiatea were isolated. Those of the latter island retain the dextral mode of coil, while the Moorea colonies, sinistral in nature, diminished in numbers and became more closely restricted, to survive as the single association of *P. tohiveana* existing to-day. The alternative view is not tenable, namely, that *P. tohiveana* has arisen from actual migrants from Raiatea to Moorea, or that the dextral Raiatea species have come directly from sinistral *tohiveana* progenitors, transported from Moorea. The conclusion so briefly stated is supported by many bodies of evidence, which will be presented fully in the later detailed discussion of the species of Moorea.

PARTULA OLYMPIA CRAMPTON

The last species to be mentioned is another new discovery, and it is sinistral like *P. tohiveana* and *P. dendroica*. It was first found in 1919 in a high area of forest on the inward face of Mt. Mouaputa and nowhere else in Moorea (Plate 5C). Like the foregoing, it exists in unusually sparse numbers; indeed, it would seem that it is in grave danger of extinction.

Paralleling *tohiveana* in another respect, the species displays several differentiated color-types, as follows: (a) uniform fleshy-corneous (Plate 5C); (b) uniform medium brown; (c) the same with a median band of color on the apical whorls only; (d) with a vague median band over all of the whorls (Plate 5C), and (e) with two re-

volving bands of brown, weak and faintly-defined. Again the point of note is that the species is clearly composite as regards the factors of color, even under the identical conditions of one environment.

Some of the distinctive features recall *P. mooreana*, and it may well be that *olympia* and *mooreana* are related in ancestry. If so, the animals of this stock have completely disappeared between the small area where *olympia* is now found and the distant region of Vaianai from which *mooreana* so recently began its extension and differentiation in the ways that have been described.

CONCLUSION

The present investigation of the species of *Partula* living in Moorea comprises a comparison of the conditions which were found in 1907 and 1909 with what Garrett described for earlier decades, and also a second comparison of the later situations in 1919 and 1923 with my own first observations. In general terms, the changes which have occurred during the second time period are the same in nature as those which had taken place during the longer first interval.

The changes in question are of two kinds, geographical and constitutional, of which the latter are by far the most significant in connection with the problems of specific differentiation. It is by no means unimportant that exactly the same kinds of change have been demonstrated in some of the species of Tahiti.

When the several species of Moorea are brought together, they form a strikingly consistent series whose terms are mutually explanatory in various respects. *Partula taeniata* stands at the one extreme, with the widest spread and the highest degree of colonial diversification, both of which mark it as a species of long standing. This is followed by *Partula suturalis*, which has extended its range and gained greater complexity only in recent decades. *Partula mooreana* has accomplished results that are the same in principle, in even less remote

years and to lesser degrees. *Partula mirabilis* is particularly significant as the next term, because its small numbers and local restriction prevented Garrett from finding it, yet to-day it rivals *mooreana* in its range and internal diversity. Near the other extreme is *Partula dendroica* whose extension has only just begun; while finally *Partula olympia* and *Partula tohiveana* exist in small single colonies and in sparse numbers, thus presenting a condition like that of other species before they had started to multiply, to diversify and to disperse more widely.

That mutation is a real and a contemporaneous process is proved in the first place by the existence of divergent individuals of adult growth, such as the two sinistral examples of *taeniata*, the dextral specimens of *mooreana* and the sinistral representatives of *mirabilis*. If clearer proof were possible, it is provided by the mutant young within the brood-pouch of a standard type of adult, as in the case of the dextral *mooreana* borne by a reversed parent.

Further summary does not seem expedient in advance of a full presentation of the facts. There are many problems that come directly into question, the one of paramount importance being that which is concerned with the possible participation of the "environment" in the stimulation of the various species to produce their novel forms; as the facts stand at present, the "environment" appears to have been negligible as regards a causal relation to the episodes of organic differentiation actually demonstrated.

THE ISOLATION OF A PATTERN VARIETY IN PIEBALD HOUSE MICE

DR. L. C. DUNN AND G. B. DURHAM
STORRS AGRICULTURAL EXPERIMENT STATION¹ AND
CONNECTICUT AGRICULTURAL COLLEGE

IN an earlier paper (Dunn, 1920) the occurrence of what appeared to be distinct pattern types of white-spotted (piebald) house mice was noted; and a preliminary description of the variations and of their behavior under inbreeding was given. The attempt to isolate these varieties has been continued, and it is the purpose of this note to report the results obtained by inbreeding two of these pattern varieties for twelve and seven generations, respectively; together with data resulting from crosses between them and from crosses of each type with the wild form.

The variations to be described arose in a random bred stock of piebald mice which were obtained from a fancier in 1919.²

Of the 65 piebald mice purchased a few were noted as having dorsal white spotting on the face or head only (Fig. 1) and two were noted as being spotted only in a white band around the body between the fore and hind limbs (Fig. 2). The first type was designated as *white face spotting*; the second as *belt*. These were used in other experiments involving crosses with self-colored mice. From such crosses there appeared in later generations well-defined white-faced and belted types, which were saved for further study.

The first experiment consisted of inbreeding, by brother-sister matings, the progeny of several pairs of white-faced and of belted mice. Matings between litter

¹ Contributions in Genetics No. 26.

² The first two generations of the experiments to be reported were carried on at the Bussey Institution, Harvard University, and the stock was obtained through the kindness of Professor W. E. Castle.



FIG. 1. The white-faced variety of piebald; a parent of one of the inbred lines.

mates were made in several lines for three generations, after which the lines which conformed most closely to the type desired were continued and the others were abandoned. In the white-faced lines, only those mice were selected for breeding which had dorsal white spotting on the face only, either as a blaze, a white nose or a wholly white face. The last type was preferred. In the belted lines selection was toward a well-defined continuous belt of white, although so few of this type were obtained that the actual criterion became "spotting in the position of

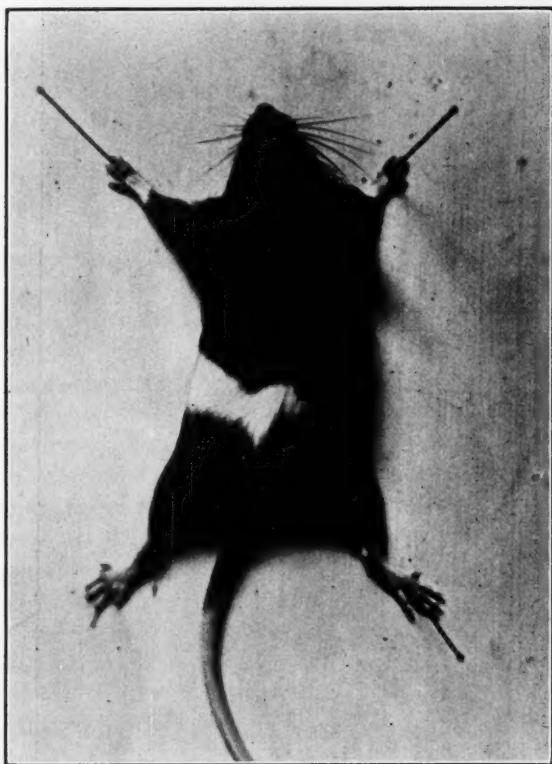


FIG. 2. A belted piebald; ancestor of one of the inbred lines.

the belt only." Shorthand descriptions of the spotting pattern and a sketch on a standard diagram were made of each mouse at about one month of age.

THE WHITE-FACED TYPE

The results of inbreeding the white-faced types are given in Table I. The P_1 generation consists of offspring of pairs selected as good white-face types. The parents were in general not closely related. These progeny were bred brother by sister to produce the F_1 inbred generation. The chief line, No. 46 of our records, is sepa-

rated in the table from lines originating from other pairs. In line 46 several collateral lines were carried to the sixth generation. Thereafter all mice in this line are descended by straight brother-sister matings from one pair in the sixth generation.

TABLE I

RESULTS OF INBREEDING (BROTHER \times SISTER) THE OFFSPRING OF SINGLE PAIRS OF PIEBALD MICE OF THE WHITE-FACE TYPE

Generation	Number of offspring		Offspring with white face only		Offspring with white face and other spotting	
	Line 46	All Lines	Line 46	All Lines	Line 46	All Lines
P ₁	4	108	4	99	0	9
F ₁	6	68	6	66	0	2
F ₂	20	35	19	34	1	1
F ₃	88	96	84	92	4	4
F ₄	84		78		6	
F ₅	32		32		0	
F ₆	48		46		2	
F ₇	56		56		0	
F ₈	43		42		1	
F ₉	33		30		3	
F ₁₀	14		9		5	
F ₁₁	13		12		1	
F ₁₂	14		14		0	
F ₁₃	17		17		0	
F ₁₄	3		3		0	
	475	664	452	630	23 ³	34

It is apparent from this table that the white-faced variation bred practically true from the beginning. All the progeny of all lines were spotted on the face. In addition 34 mice out of the 664 reared were spotted elsewhere on the dorsal surface. Of these latter, 21 showed only a few white hairs or a small spot on the neck behind the ears. This appeared to be merely a fluctuation or extension of

³ The mice showing white spotting on other parts of the upper surface in addition to the face consisted in Line 46 of 16 with some white on the neck (partial collar), four with a few white hairs in the center of the back, one with a small white spot on the shoulder, one with a small spot on neck and one side, and one with a partial belt. In the other lines there were five with neck spotting in addition to the white face, four with small spots in the position of the belt and two with both neck and belt spotting.

the white-face type. This leaves but 13 exceptions, which were spotted on parts other than the head or neck, and in these white hairs or small spots appeared only on the back and sides. These spots could often be interpreted as upward extensions of the ventral spotted area, which is very variable. These variations appeared to be non-heritable. Two mice with spotting on the back in addition to the face spotting produced when bred with white-faced sibs only white-faced descendants in subsequent inbred generations. Even in the tenth generation of inbreeding, five out of 14 mice showed these slight departures from the white-face type, which is added evidence that they probably occur at random in homozygous white-faced piebald mice and are non-genetic in origin.



FIG. 3. A typical white-faced piebald from the 14th generation.

On the whole the white-faced type appears to be a distinct true breeding variety of piebald subject to minor non-genetic fluctuations (*cf.* Fig. 3 for present appearance of the white-faced variety).

THE BELTED TYPE

The mice selected from the random bred piebald stock as originators of belt lines all showed well-defined white belts extending across the dorsal surface between the neck and the hips and joining the ventral spotting on both sides (Fig. 2). Several pairs of these belted mice were mated regardless of relationship and their progeny used as parents of several inbred lines. Only those progeny were selected for breeding which showed some white spotting on the back between the shoulders and hips, those approaching most nearly to the true belt type being preferred. Very few true belts were obtained in any generation, and our object became to eliminate spotting elsewhere than in the mid-dorsal region.

The results of the inbreeding and selection on this criterion are given in Table II. Under "belt spotting only" are listed those mice which had dorsal white spotting in the position of the belt only. These were of various types (Fig. 4). A few had good belts; more had partial or broken or double belts and many had a small white spot in the center of the back. Under Line 55 are listed all the offspring of a single pair of P_1 mice descended by single brother-sister matings. Under "all lines" are listed several different "belt" lines through the third generation, and the collaterals of Line 55 thereafter.

The proportion of mice with spotting in the position of the belt only was very low in the early generations. In Line 55 only eight of the 29 offspring of the original belted pair showed any approach to the belt type. The others were variably spotted on back, face, head and neck regions. The only generalization we can make concerning these other types is that none showed the white-face condition alone; and that all showed spotting in the central dorsal region, accompanied by some spotting else-

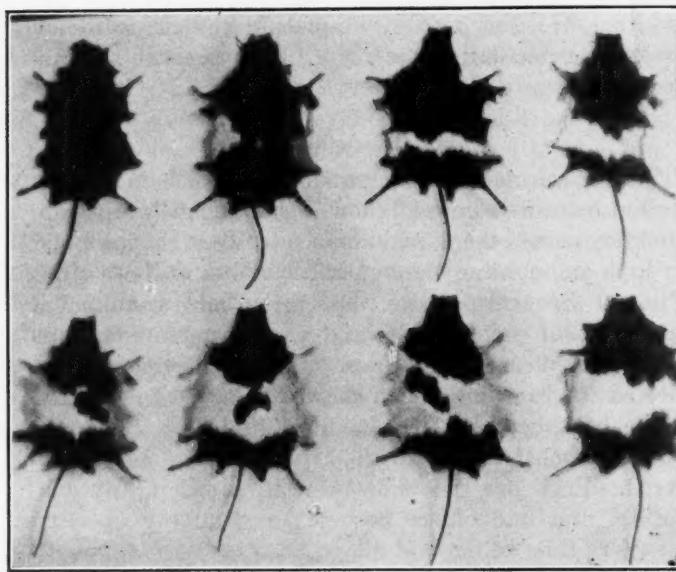


FIG. 4. Skins showing some of the variations encountered in the "belted" type of piebald. The skin of a self colored (unspotted) mouse is shown for comparison in the upper left hand corner.

TABLE II

RESULTS OF INBREEDING THE OFFSPRING OF SINGLE PAIRS OF PIEBALD MICE OF THE BELTED TYPE

Generation	Number of offspring		Offspring with belt spotting only		Offspring with belt and other spotting	
	Line 55	All Lines	Line 55	All Lines	Line 55	All Lines
P ₁	29	90	8	35	21	56
F ₁	15	122	8	62	7	60
F ₂	19	88	15	49	4	39
F ₃	13	36	11	31	2	5
F ₄	47	77 ⁴	39	65	8	12
F ₅	27	48 ⁴	25	40	2	8
F ₆	28	58 ⁴	27	51	1	7
F ₇	19	48 ⁴	19	47	0	1
F ₈	26	26	25	25	1	1
	—	—	—	—	—	—
	221	593	177	404	44	189

⁴ Collaterals of Line 55.

where. The proportions of belt types increased and the proportions of other types decreased under inbreeding, until in the seventh generation only one out of the 48 mice showed spotting elsewhere than in the belt position. It can not be said, however, that we have produced a true breeding belted type of piebald mice, for the proportion of typically belted mice is still low after seven generations of inbreeding and there is great variability in the amount and position of the dorsal spots (Fig. 4). The most that can be claimed is that inbreeding accompanied by selection has produced a type which is not spotted on the face or elsewhere than in the central dorsal region. These results are, therefore, somewhat at variance with those obtained in the white-face inbreeding, since the white-face type was easily isolated and fixed and appeared therefore to rest on a relatively simple genetic basis, while the true belt pattern appears to be either a random expression of diffuse mid-dorsal spotting or to depend on a more complex genetic basis.

From the results of both inbreeding experiments it may be concluded that some of the variations in the spotting patterns of piebald mice are genetic, and that two of them—the white-face, and the mid-dorsal non-white-face type—have been isolated by inbreeding.

AMOUNT OF SPOTTING IN WHITE-FACE AND BELTED TYPES

All mice recorded in the above experiments were described also with respect to the amount of dorsal white spotting. The same percentage scale described in a previous paper (Dunn, 1920) was used. The results for the two chief inbred lines are given in Table III.

The average percentage of the dorsal surface which was white was much less in the white-faced than in the belted parents. The averages for the white-face P_1 and F_1 generations are based on too small numbers to be reliable. After the second generation the amount of white spotting in this line declined quite steadily.

This apparently represents a real diminution in the amount of white spotting and not a change in the meth-

TABLE III
AVERAGE AMOUNT AND VARIABILITY OF DORSAL WHITE SPOTTING OF TWO
INBRED LINES OF PIEBALD MICE

Generation	Line 46 (White Face)				Line 55 (Belted)							
	Mean		Mean		N.	per cent.	S. D.	C. V.	N.	per cent.	S. D.	C. V.
P ₁	4	9.5	4.9	51.6	29	17.3	7.7	44.5				
F ₁	6	14.3	1.9	13.3	15	18.0	9.3	51.7				
F ₂	19	13.4	6.6	49.3	19	22.0	12.5	56.8				
F ₃	88	12.0	3.7	30.8	13	13.9	12.8	92.1				
F ₄	84	10.0	3.9	39.0	47	15.8	11.4	72.1				
F ₅	32	10.3	3.4	33.0	27	10.1	7.1	70.3				
F ₆	48	9.8	4.2 ⁵	42.9	28	13.6	8.1	59.5				
F ₇	56	7.5	2.6	34.7	19	15.9	7.3	45.9				
F ₈	43	7.0	2.6	37.1								
F ₉	33	6.7	2.5	37.3								

ods of estimating the size of the white areas. This is supported by comparison of the white-faced mice of the present (fourteenth) generation with photographic records of those in the parental and early generations (*cf.* Figs. 1 and 3) and by checking the numerical estimates against the standard sketch record which we made for each mouse at weaning time. The selection practiced was intended to fix a pronounced and extensive white face in this type, but we were also influenced by a desire to avoid extension of the spotting to the neck or other adjacent regions. The latter circumstance and the chance selection of a line with an inherent tendency to show but little spotting on the face probably accounts for much of the decline noted. Changes in the amount of white spotting were most marked in the white-faced line, the belted line varying irregularly from generation to generation.

Variation in the amount of spotting in these inbred mice is considerably less than in the random stock of piebalds from which they are descended. The coefficient of variation of 473 stock piebalds was about 88 per cent.

⁵ Variability increased by a single aberrant individual with 26 per cent. of white spotting due possibly to mutation.

(Dunn, 1920, p. 483), while for the white-faced line it is less than half as great and for the belted line about two thirds as great. These lines are, therefore, genetically different from random bred piebalds not only in localization, but in amount of spotting as well. Further inbreeding appears not to have reduced further the variability of spotting in the white-faced line. The standard deviation (Table II) appears to have decreased under inbreeding, but that this is due entirely to decrease in the mean amount of spotting is shown by the fact that the coefficient of variation has shown no significant change under inbreeding. Variations in the small amount of spotting occurring within the inbred white-faced line appear, therefore, to be non-genetic. In the belted line, although the numbers are small, variability appears to have declined after the third generation, indicating that some of the variations in the larger amounts of spotting characteristic of this line are produced by heritable factors. Consideration of these data and observation of the animals indicate that the white-face line has now (fourteenth inbred generation) reached the limit of reduction in variability; and that the variability remaining (between 30 and 40 per cent.) measures the amount of non-genetic variability occurring in the expression of the piebald gene.

CROSSES INVOLVING WHITE-FACED AND BELTED MICE

The cross of belted and white-faced types has been made reciprocally at three different stages of inbreeding. The reciprocal crosses have given substantially the same results. A cross when the belt and white-face lines were in the second-third generations produced an F_1 generation consisting of twelve white-faced piebalds. These inbred produced a second generation of 52 white-faced, 16 belted, two with both white face and belt spotting and three with no dorsal spotting whatever. A backcross of F_1 mice to the belted parent produced eight white-faced, four belted, one white-faced and belted and two with no

dorsal spotting. A cross in the fifth-seventh inbred generation produced 24 white-faced, two with white face and belt and three with no dorsal spotting. These when inbred produced in F_2 25 white-faced, 20 with white-face and belt spotting, six belted and two with no dorsal white. A cross in the twelfth generation has produced two white-faced, seven with no dorsal spotting, three with white face and belt and two with belt only. No second generation has been reared from the last cross, since the variation in evidence in the first generation indicates that one or both of the parents were not homozygous or that other factors have entered to complicate the results. Adding together the results of the first two crosses gives the following totals:

CROSS OF WHITE-FACE AND BELT PIEBALDS				
White Face	Belt	White Face and Belt	No Dorsal Spotting	
F_1 36	—	2	3	
F_2 77	22	22	5	

It is apparent that in these crosses the "white-faced" condition behaved as a dominant in inheritance and that in the second generation it segregated from the alternative condition "no white spotting on the face" in a majority of the cases. The ratios obtained are discussed in a later section.

CROSSES WITH THE WILD TYPE

As additional tests of the inheritance of the white-faced and belted conditions we have crossed both kinds of mice with the same strain of wild house mice. The wild mice were trapped in a barn at a considerable distance from any domesticated mice, and have never shown any evidence of intermixture with domesticated varieties. The mice of this strain have been invariably self-colored with the black agouti coat which is typical of the wild form. The cross of white-faced piebald mice from the fifth-seventh generations of Line 46 with the wild stock produced in F_1 only black agouti self-colored mice of the

wild type. In F_2 of the 45 piebald mice which appeared as recessive segregates all except three were spotted on the face only in the white-faced pattern. In the three exceptions (which occurred in the offspring of one F_1 mother) the white spotting of the face extended backward between the ears and over one or both shoulders in the form of a partial collar. One of these when bred back to his F_1 self mother produced six self and seven piebald young. Of the piebalds three showed the ordinary white-faced spotting, while four reproduced the extended spotting of the father, indicating that the genotype of this female included factors which tended to increase the amount of white in her piebald descendants. The white-faced pattern has, therefore, been passed through a wild self-colored race and extracted in its original condition with the exception noted.

Individuals of the "belted" line (No. 55) crossed with the wild race produced all wild type self mice in F_1 and in F_2 of the 37 piebalds born, 23 were of the belt type, nine had both belt and white-face spotting, three had white-face spotting only and two had no dorsal white spotting. The belted parents used were true belts from the early (F_1 and F_2) generations of inbreeding and the proportion of offspring from the wild cross showing white-face in addition to belt spotting is about the same as occurred in pure belt matings. We do not believe the tendency for white spotting to be exhibited principally in the belt region has been altered by the cross. One of the F_2 white-faced mice out of this cross was bred to a sister with belt spotting and a small white blaze between the eyes. Of their 26 offspring, nine were of the belt type, 16 had both blaze and belt spotting, and one had no dorsal spotting. No mice with only white-face spotting appeared, so that the small amount of white-face spotting in this mouse appeared to be distinct from the usual type of white face and had probably not been introduced by crossing with the wild type.

DISCUSSION

The evidence from the inbreeding of white-faced piebald mice and from crossing them with non-white-faced piebalds and with wild mice leaves little doubt that "white-face" is a distinct true-breeding variety of piebald. It appears to contain a gene (or genes) for the restriction of white spotting to the head and face, and is therefore expressed only in the presence of the gene for piebald or recessive white spotting. Aside from the probability that this modifying gene acts as a dominant little is known of its inheritance. It has been passed through self-colored mice and recovered without any significant alteration. It has shown evidence of segregating from crosses of white-faced by "belt" mice, although the F_2 ratios obtained from this cross are inconclusive because of the appearance in the second generation of a number of mice with *both* white-face and "belt" spotting. Such mice have frequently appeared in the progeny of "belt" parents and may contain recessive modifying genes distinct from those found in the true breeding white-face lines. When bred, such "white-face and belt" mice have not behaved as ordinary hybrids between white-face and "belt" types, since they have never produced mice with white spotting on the face only. With only the present evidence at hand they can not be satisfactorily explained. It is otherwise with the other type encountered, *viz.*, mice with no white spotting on the dorsal surface. These have frequently occurred in many forms of piebald and apparently contain modifying genes which reduce the general *amount* of white spotting (Dunn, 1920). They are probably very dark piebalds which are unable to express any dorsal spotting pattern and are thus similar to the dark piebald (hooded) rats obtained by Castle (1916).

We are unable to make any final statements concerning the "belt" pattern. This has not become fixed under inbreeding, except that it does not produce mice of the white-face type.

CONCLUSION

The isolation of at least one true-breeding pattern variety from a variable stock of piebald mice demonstrates that a portion of the great variability in piebald spotting is due to genes affecting the *distribution* or localization of spotting in the coat. Experiments reported previously (1920) indicated that other genes are responsible for a part of the variability in the general *amount* of spotting. It is probable, then, that the various types of piebald mice owe their origin in part to heritable variations in other genes modifying the expression of the principal gene concerned with recessive white spotting.

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THE RELATION BETWEEN PREVIOUS SEXUAL
REPRODUCTION AND THE PRODUC-
TION OF MALE OFFSPRING
IN MOINA MACROCOPA¹

DR. A. M. BANTA
COLD SPRING HARBOR, N. Y.

WEISMANN ('79) set forth the hypothesis that in Cladocera there is an innate sexual cycle quite independent of environmental influences. Later workers have taken various attitudes toward this theory ranging from (a) complete acceptance, (Keilhack, '06; Kuttner, '09; van Herwerden, '18); through (b) a modified acceptance—belief in an internal sexual cycle which, however, is more or less subject to environmental modification or control (Issakowitzsch, '08; Woltereck, '09; McClendon, '10; Papanicolau, '10; Grosvenor and Smith, '13; Scharfenberg, '14); to (c) a belief in the direct opposite of Weismann's theory—that sexual manifestations in Cladocera are not influenced by internal factors but are called forth solely by environmental influences.

Weldon ('09, p. 50) by inference suggests and possibly he meant to subscribe to this last view. Later the writer ('13, '14) and Agar ('14) came out squarely against the Weismannian hypothesis. The writer in his first report had reared thirteen lines of *Daphnia* for from 25 to 33 parthenogenetic generations. In the second paper ('14) the writer reported 100 parthenogenetic generations of *Daphnia pulex* and 76 generations of *Simocephalus*. Agar based his conclusions upon the rearing of *Simocephalus vetulus* for 46 generations by parthenogenesis and without the occurrence of degenerate forms or of more than the sporadic occurrence of males. Later ('15) the writer published a brief note stating the results of an

¹ Assisted by Kathleen Gavin.

experiment which showed that the reproductive vigor of old laboratory lines, parthenogenetic for 127 generations, was substantially the same as that of newer lines just brought into the laboratory.

At the present time stocks of several species of Cladocera, long in the laboratory and exclusively parthenogenetic for long periods of time (some more than 500 generations), show no reduction in vigor or proneness to produce either sexual forms or abnormalities. Such histories seem inconsistent with an innate sexual cycle.

We have recently hatched young (females) from fertilized (sexual) eggs of *Moina macrocoda*.² If there were really an internal sexual cycle in any sense of the term, it would seem that as parthenogenesis continued the stock would become more and more prone to produce males and ephippial (sexual) eggs; or at least that strains just derived from sexual eggs should be less readily caused to go into sexual reproduction than strains parthenogenetic for many generations.

In order to get evidence on this point two stocks were utilized. The one was from the parent line of *Moina macrocoda* (Line 1012) in its 294th to 301st generation of laboratory descent solely by parthenogenesis. The other was stock in its 1st to 7th generation of descent by parthenogenesis from lines derived by sexual reproduction from Line 1012. These two stocks were simultaneously subjected to environmental conditions known to call forth the production of males. The means employed to cause the production of males is the simple expedient of crowding the mothers in the culture bottles (cf. Grosvenor and Smith, 1913; Banta and Brown, 1923). Since environmental influences are utilized, it is desirable to set forth some of the details of the conditions of the experiments.

In preparation for the first of these experiments (Experiment 111, started January 14, 1922) newly released

² These ex-ephippial females themselves produced males among their offspring.

parthenogenetic young of stock in its second parthenogenetic generation and newly released young stock in its 293rd³ consecutive parthenogenetic generation were isolated in similar culture bottles on the same day, given the same food and otherwise treated as nearly alike as possible. When these produced young, large broods which had been released from the mothers' brood-chamber near the same time were taken for use in starting the experiment. Hence, all the broods of young employed as mothers in an experiment were within an hour or two of the same age and were from mothers which had been subjected to identical treatment from birth. In addition to the care given the grandmothers and the pains taken in the selection of the mothers, every effort was made to accord identical treatment to all the material concerned in an experiment. All the future mothers were placed in the culture bottles at the same time; an equal amount (75 cc) of culture water, from the same culture jar, was placed in each bottle; and the individuals were in every way treated alike, except that some from each brood of both new and old parthenogenetic stocks were crowded —10 in a bottle—while the others were in individual bottles.

In Experiment 111 three broods from the third generation of three new strains of *Moina macrocopa* were used in making up the 8 crowded and the 10 uncrowded bottles of the new stock; while two broods of the 294th generation of Line 1012 provided the material for the 4 crowded and the 6 uncrowded bottles of the old stock. The data of this experiment are shown in Table 1, in which the numbers of female and male young produced in each bottle are indicated by broods.

From inspection of this table it may be seen that the uncrowded mothers of the new stock produced 0, 7.7, 37.1, and 0 per cent. males in their first to fourth broods,

³ It was the 293rd *laboratory* generation. We do not know when sexual reproduction may have occurred previously to the taking of this stock into the laboratory.

respectively, or 12.4 per cent. males for the total for the four broods (1,113 young); while the old stock produced 0, 30.9, 0 and 28.7 per cent. males for the first four broods, respectively, or 13.6 per cent. males for all (580 individuals). While there is considerable variation by individual broods, the percentage for the entire four broods for the new and old stocks are nearly the same—12.4 per cent. and 13.6 per cent. The percentages of males in the first, second and third broods in crowded bottles (81 mothers in 8 bottles) of the new stock are 24.0, 64.6 and 40.4 or for the lot (2,205 ♀s and 1,486 ♂s) 40.3 per cent. These compare with corresponding percentages of 19.5, 73.7 and 27.6 for the different broods and 37.1 per cent. for all the broods (1,185 ♀ and 700 ♂s) of the old stock (39 mothers in 4 bottles).

In spite of variations the percentages of males produced in this experiment by the new and the old stocks (both by crowded and unerowded mothers) are so nearly the same as to indicate no significant difference in the incidence of males between stock which had experienced sexual reproduction 3 generations previously and stock which had last passed through sexual reproduction at least 294 generations previously.

Two other similarly extensive experiments were conducted with new and old parthenogenetic stock. In one of these experiments new stock in the 7th parthenogenetic generation and in the other case stock of the first parthenogenetic generation was employed. Brief summaries of the data for these experiments, together with that for Experiment 111 (detailed in Table 1) are given in Table 2. This table consists of four portions, the first and second of which show summaries of data for new and old unerowded bottles and the third and fourth for new and old stock in crowded bottles.

Of the 1,865 young produced by mothers of the new stock in unerowded bottles in these three experiments 178 or 9.54 per cent. were males. Of the 1,460 young produced by similarly treated old stock 147 or 10.07 per cent.

TABLE I—DATA OF EXPERIMENT III
New *Moina macrocycpa*. Lines 1133, 1134, and 1135. (3rd generation).

Line No.	Bottle No.	Uncrowded Mothers				Crowded Mothers			
		First Brood	Second Brood	Third Brood	Fourth Brood	First Brood	Second Brood	Third Brood	% ♂'s
1133	1	♀ 17 0	♀ 32 0	♀ 34 0	♀ 24 0	♀ 157 0	♀ 23 0	♀ 9 0	38.1
	2	17 0	27 0	0 28	31 0	163 41	59 85	75 52	37.5
1134	3	23 0	34 0	28 0	31 0	131 45	37 95	61 55	46.0
	4	21 0	34 0	0 27	32 0	111 107	75 31	87 53	41.2
1135	5	22 0	29 0	32 0	34 0	188 49	59 63	64 53	34.7
	6	23 0	35 0	3 26	33 0				
	7	20 0	29 2	32 0	28 0				
	8	15 0	27 2	41 0	37 0	174 27	31 132	79 52	42.6
	9	20 0	0 21	28 0	32 0	183 13	23 114	97 25	33.4
	10	17 0	30 0	31 0	26 0	118 70	72 71	44 84	49.0
Totals		195 0	277 23	195 115	308 0	1225 387	379 691	601 408	
Average Brood		19.5	30.0	31.0	30.8	19.9	13.5	12.9	
Percent ♂'s		0.0	7.7	37.1	0.0	24.0	64.6	40.4	
Total Young			1113						3691
Average brood per mother			27.8						15.5
Average percentage ♂'s			12.4						40.3

TABLE I.—Continued
Old *Moina macrocera*. Line 1012. (294th generation.)

1012	1	25 0	Died	32 0	33 0	212 8	17 142	110 13	32.5
	2	20 0	35 0	34 0	0 37	132 19	35 93	88 12	32.7
	3	25 0	3 0	34 0	3 0	93 124	72 37	49 131	57.7
	4	27 0	18 11	33 0	3 0	199 3	15 118	163 0	24.3
	5	26 0	0 31	32 0	37 0				
	6	27 0	38 0	34 0	19 0				
Totals		150 0	94 42	165 0	92 37	636 154	139 390	410 156	
Average Brood		25.0	27.2	33.0	25.8	20.3	14.3	15.3	
Percent ♂'s		0.0	30.9	0.0	28.7	19.5	73.7	27.6	
Total young		580					1885		
Average Brood per mother			27.6				16.7		
Average percentage ♂'s			13.6				37.1		

were males. Similar comparisons of the total numbers of young from crowded mothers of all three experiments shows that the new stock produced 4,571 females to 2,735 males or 37.43 per cent. males, while the old stock produced 3,628 females to 2,169 males or 37.42 per cent. males. Hence, totals of substantial numbers of young (16,428 young from 323 mothers) from new and from old stock reared both in crowded and in uncrowded conditions show approximately the same percentages of males for the new and for the old stock.⁴

Further examination of these experiments serves to give additional emphasis to this similarity of male production in new and old parthenogenetic stocks. Individual experiments show fairly close agreement in male percentage between the new and the old stock, whether the comparison is made between uncrowded or crowded stock. Experiment 111, already considered, indicates this. Comparing similar figures for Experiment 112: the new stock, uncrowded, produced 7.3 per cent. males; the old, 10.4 per cent. males; and in crowded bottles the new stock produced 37.2 per cent. and the old 46.3 per cent. males. In Experiment 117 the uncrowded stock died and could not be followed beyond the first broods. The crowded mothers produced 31.9 and 27.2 per cent. males in the new and the old stocks, respectively. Hence, in these experiments all the comparisons of male production between new and old stocks, whether isolated or crowded, show substantially the same percentages of males.⁵

⁴ Undoubtedly the remarkably close agreement in these percentages, 37.43 and 37.42, is a coincidence. One would not expect a second extensive series of such experiments to give so nearly precisely the same percentages, though they would not be significantly different.

⁵ Certain points of minor interest are suggested by further examination of Table 2, although their significance is not so clear.

(1) The uncrowded new stock in both Experiment 111 and Experiment 112 produced fewer males in second broods than the old stock (although the reverse was true for third broods); while in the crowded bottles (in which male production begins in first broods) the new stock produced a larger percentage of males in all three experiments in first broods than the old stock.

On two occasions we hatched a number of ex-ephippial young *Moina macrocoda* on the same day. Although we did not then have at hand newly released parthenogenetic young of the old stock to use in conducting a comparative experiment, such as those discussed above, we crowded the newly hatched (ex-ephippial) young to see if they would produce a considerable percentage of males. In Experiment 118 (March 4, 1922) ten such crowded mothers produced 50 ♀s and 53 ♂s in their first broods and 34 ♀s and 8 ♂s in second broods. This represented male percentages of 51.5 and 19 for the first and second broods, respectively, or 42.1 per cent. for the two broods considered together. In Experiment 126 (September 6, 1922) 14 ex-ephippial mothers were crowded in a single bottle and in their first broods produced 36 ♀s and 76 ♂s or 67.9 per cent. males.

While these last two experiments contain only a little data, they are of interest, inasmuch as they represent two separate lots of material and were hatched at different times. In crowded bottles they produced characteristically high percentages of males in their first broods, regardless of the fact that they had just hatched from sexual eggs.

Hence, not only new stock in the 1st, 3rd and 7th parthenogenetic generations but even those individuals, themselves, hatched from sexual eggs produced (under appropriate conditions) as large percentages of males as stock which had not had sexual reproduction for 300 or more generations.⁶ It would, therefore, seem clear that there are no significant differences in male-produc-

(2) The new stock, both in crowded and uncrowded bottles, produced smaller first broods than the old stock. The six differences (between the uncrowded new and old stocks and between crowded new and old stocks in three separate experiments) are all differences in the same direction. This can scarcely seem a mere chance occurrence.

⁶ The five experiments discussed are not selected experiments. On the contrary, they represent all the experiments conducted to date in testing the male production of stock which had recently had sexual reproduction. There is every reason to believe that these results are typical and that like experiments would at any time give similar results.

TABLE II.—SUMMARY OF DATA OF EXPERIMENTS 111, 112, AND 117
 (Started Jan. 14, Feb. 2, and March 3, 1922, respectively.)
 Comparison of Male Production in New and Old Parthenogenetic Stocks of *Moina m.*
 Uncrowded New Stock Crowded Old Stock

TABLE 2—Continued

Crowded New Stock										Crowded Old Stock									
Exp.	Par. No.	First Brood				Second Brood				Third Brood				All Broods					
		♀	♂	Av.	Av.	♀	♂	Av.	Av.	♀	♂	Av.	Av.	♀	♂	Av.	Av.		
Gen. Bot.	No.	Gen. Bot.	♂	Av. Brd.	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.
111	3	8	1225	387	19.9	24.0	379	691	13.5	64.6	601	408	12.9	40.4	2205	1486	15.5	40.3	
111	7	4	386	426	21.4	52.5	459	85	14.7	15.6	300	167	15.1	35.8	1145	678	17.2	37.2	
111	1	4	751	122	21.8	14.0	224	114	9.3	33.7	246	335	16.1	57.7	1221	571	16.0	31.9	
Totals & Averages	16	2362	935	20.74	28.4	1062	890	12.84	45.6	1147	910	14.18	44.2	4571	2735	16.02	37.43		
Crowded New Stock										Crowded Old Stock									
Exp.	Par. No.	♀	♂	Av.	Av.	♀	♂	Av.	Av.	♀	♂	Av.	Av.	♀	♂	Av.	Av.		
Gen. Bot.	No.	Gen. Bot.	♂	Av. Brd.	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.	♂	Av. Brd.
111	294	4	636	154	20.3	19.5	139	390	14.3	71.0	410	156	15.3	27.6	1185	700	16.7	37.1	
111	298	4	582	321	23.2	35.5	195	326	13.7	62.6	360	335	18.8	48.2	1137	982	18.6	46.3	
111	306	4	933	52	25.1	5.2	53	370	10.6	87.5	300	65	9.1	17.8	1306	487	14.9	27.2	
Totals & Averages	12	2171	527	22.86	19.5	387	1086	12.8	73.7	1070	556	14.26	34.1	3628	2169	16.7	37.42		

*The data for 'all broods' of the uncrowded stock of Experiment 111 include data for fourth broods which are given in Table I, but not in this Table.

ing propensity between stocks which have recently had sexual reproduction and stocks which have undergone parthenogenetic reproduction exclusively for a long series of generations.

The facts would seem to warrant the conclusion that exclusively parthenogenetic reproduction for an indefinite number of generations does not modify the tendency to produce males in *Moina macrocera*.

The former evidence against an innate sexual cycle in Cladocera, *i.e.* (1) that parthenogenetic reproduction may be continued for hundreds of generations, and presumably indefinitely, without the intervention of sexual reproduction and (2) that sexual forms may be called forth at will in many (at least) forms of Cladocera, is now supplemented by the results of the experiments here recorded which indicate that stock recently derived from sexual eggs is no less (or more) prone to produce males under appropriate environmental conditions than stock which has descended 300 generations since last undergoing sexual reproduction.

ARTHUR M. BANTA

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DO THE CHARACTERISTICS OF PREHISTORIC HUMAN REMAINS IMPLY A COMMON ANCESTRY FOR MAN AND APES?

PROFESSOR WILSON D. WALLIS

UNIVERSITY OF MINNESOTA

SINCE resemblance to the apes increases as we trace back man's ancestry into neolithic times, the later paleolithic, the earlier paleolithic and those still earlier stages represented by the remains from Heidelberg, Piltown, Java, this resemblance which intensifies with age has been accepted as pointing to a common ancestry for man and apes. There may be other abundant evidence for supposing such a common ancestry, but we believe the evidence of prehistoric human remains does not justify that inference, though of course it does not discountenance it. We base this conclusion on the fact, if fact it be, that practically all the changes in man's structure traceable through prehistoric remains are the result of changes in food and habits. Let us see what these changes are and what shifts in man's diet or habits might account for them.

The most notable changes are those in the skull. Briefly, the story of change from prehistoric to modern man is: A higher frontal region; increased bregmatic height; smaller superciliary ridges; increased head width; less facial projection; lessened height of orbits and a shifting of the transverse diameter downward laterally; a more oval palate; smaller teeth; diminished size of third molar; less specialization in type of teeth; shorter, wider, and more ovoid mandible; increased chin prominence; smaller ramus; decrease in size of condyles; decrease in distance between condyle and coronoid process; in general a greater smoothness, less prominent

bony protuberances, less of the "savageness" of appearance which is to be noted in apes.¹

Though there is evolution in type this evolution is result rather than cause. The change in type is notable, but we believe there is reason to assign it to change in function, to use and disuse.

Practically all the above-mentioned features of the skull are intimately linked together, so that scarcely can one change without change being reflected in the others, some, of course, reflecting the change more immediately and markedly than do others. If we suppose that man's diet and his manner of preparing food have changed, we have an index to most of these skull changes, provided the change has been from uncooked or poorly cooked food to better cooked, from more stringent diet to less stringent. A considerable development of the muscles concerned with chewing will bring about the type of changes which we find as we push human history further and further into the past.

It will affect most notably the region in which these muscles immediately function. With tough food and large chewing muscles is associated a large mandible with broad ramus, large condyles, heavy bony tissue. The larger teeth are accommodated to the tougher food and their greater specialization is a form of adaptation to the needs of the masticator. As larger teeth demand more alveolar space, we find elongated alveolar regions with greater sagittal diameter, giving the more prognathous and more angular mandible. The increased width of the ramus is a mechanical advantage in the leverage which the mandible must perform in chewing food, while the larger condyle affords a better resisting fulcrum and is associated with the greater side-to-side play which goes with longer mandible and the chewing of tougher food.²

¹ Regarding changes in chin region see Wallis, Wilson D., "The development of the human chin." *The Anatomical Record*, Vol. 12, No. 2, March, 1917, 315-328.

² Hawkes, E. W., and Wallis, W. D., "Notes on the Glenoid Fossa." *American Anthropologist*, Vol. XVIII (1916), 440-446.

The more forward projection of teeth in both upper and lower alveolar region is in accordance with what we find in animals which use the teeth for the mastication of tough food and no doubt is a function of mastication. The palate conforms to the mandible, with which it forms a physiological unit, however separate morphologically the two may be, hence is long and less arched. Zygomatic arches stand out for the accommodation of the large chewing muscles which pass beneath them. The adjacent walls of the skull are flattened and forced inward by the pull of muscles which of necessity is inward as well as downward, giving us an elongated skull. The temporal muscles reach far up on the skull, giving rise to a high temporal ridge; they extend forward as well as backward, giving a more prominent occipital region and a more constricted forward region, resulting on the forehead region of the skull in the elevation of the superciliary ridges and intervening glabellar region.

The facial region is constricted laterally and responds in a greater forward projection, one result being that the transverse diameter of the orbits is thrust upward outwardly, giving the horizontal transverse diameter which characterizes the apes and which is approximated in prehistoric man and some contemporary dolichocephalic peoples. In young anthropoid apes, when the chewing muscles are little developed and there is little constriction in the region posterior and inferior to the orbits, the transverse diameter of orbits is oblique, as in man, being elevated to the horizontal when temporal muscles develop and function more vigorously, thrusting in and upward the outer margins of the orbits. Constriction of outer margins of orbits gives the high orbits which we find in apes and in prehistoric human types.

Elongation of the skull increases the distance between bregma and nasion and gives the low retreating forehead and low head-breadth-height index.

That muscular pull has this result is indicated by the laboratory experiments of Arthur Thomson, conducted

on inflated canvas bags of the shape of a skull, with attachments corresponding to the chewing muscles and with variations in the pressures and pulls applied. It is further indicated by the fact that the Eskimo, a people living on raw food, have almost all the "primitive" characteristics in a more pronounced degree than do other contemporaneous peoples. Again, in the Australians, a people whose cooking of animals has attained little development—they cook the animals whole over an open fire—we find these "primitive" features. On the other hand, I am not aware that these conditions prevail among the negroes, who constitute a third group exemplifying these "primitive" traits.

As to other skeletal characters we have no evidence for the earliest remains, excepting only the femur of Java man, though there is abundant material from the much later, though still early, Neanderthal and Cro-Magnon types. Here the most notable differences have to do with the flexure of the knees and the larger posterior diameters of the lumbar vertebrae, both ape-like characteristics. A stooping posture can be inferred from the shift in plane of articular surfaces at the head of the femur and on the lower end of the femur, the upper articular surface of the tibia and the articulation of the tibia with the subjacent malleolus. That these differences exist is clear, but that they have evolutionary significance beyond reflecting change in form associated with change in function is not clear. We find them commonly in contemporary peoples of the lower cultures, such as Africans, Australians and others. The explanation of them is to be found in the absence of chairs in these cultures. The position of rest is that of squatting on the heels, or of sitting on the haunches with knees flexed, or other pose than that which Europeans assume when they sit. This throws the articular surface of the head of the femur further forward, throws back the articular surfaces of the lower end of the femur and the upper end of the tibia, and throws forward the articular surface at the inferior

end of the tibia and on the subjacent malleolus. The greater posterior diameter and lessened anterior diameter of the vertebrae of the lumbar region are a function of this more frequent and forcible bend forward of the vertebral column. Similar differences are found in savage tribes whose culture lacks chairs.

If the above interpretations are correct, it follows that a return to the conditions of diet and of life which characterized prehistoric man would be followed by a return to the type of prehistoric man. Yet from this transition to type more simian one could not say we were approaching a common ancestor, for, if we have one, we would be getting further away, no matter how similar the type might become.

It would be a case of similarity due to similar conditions, a convergent evolution, not a similarity due to the transmission of qualities from some common ancestor of a remote past. If this be true, it is equally true that an increase in similarities as we push back the time period does not imply common ancestry, supposing those changes are due to changes in function, to function related to diet and posture of body. Since the male of the human species resembles the anthropoid ape in nearly all these characteristics more than does the female, when we take male and female of a given group—though of necessity both sexes must be equally remote from simian-like ancestry—it seems clear that mere resemblance can not constitute an argument for phylogenetic descent. These sex differences, moreover, are in support of what we have said above, seeing that the more muscular male takes on those same simian attributes, though to a lessened degree, which are characteristic of early man. If he is more conservative of the type—though this attribute usually is assigned to the female—this is because his bodily activity is more nearly that of prehistoric man and that of his supposed relatives, the anthropoid apes.

Though this is not a critique of the theory of evolution but merely of one line of argument wherein change

of type is assumed to show common ancestry with a zoologically similar genus, we would like to point out that man, if descended from an ancestor common to apes, should in type more nearly approach that remote ancestor as we go back to earlier simian types, whereas we commonly insist that the earlier human types approximate contemporary simiae. It would seem to be of as much importance to the theory of common ancestry to show that earlier simian forms approach the type of earlier human forms. Yet it seems that they do not so approach them. The resemblances of prehistoric man hark forward to modern apes rather than back to prehistoric anthropoid ancestry. Prehistoric anthropoid forms seem to help us as little in supplying the missing link as do those prehistoric forms on which we have placed too much reliance, because an age with its mind made up to evolution of a unilinear type has seen what it has looked for. In unravelling the past can we do other than follow the methods of the geologist, who infers past changes by a study of existing forces and infers the existence of no force with which he is unacquainted? If we are correct in our interpretation, in so far as prehistoric human remains are concerned, it is not so much evolution which has given us modern man, as man who has given us his type by evolving it through physiological or functional changes growing out of changes in his culture, an evolution which he is still continuing. If the cause lies within the species it does not imply common ancestry with a morphologically and anatomically similar species, even as it is not an argument against such common ancestry.

What, then, is our conclusion with regard to the relationship between man and apes? Briefly this: A review of the similarities in structure, in blood and in use of the limbs, points to the apes as man's nearest relatives in the animal kingdom, his first cousins, if he has any. That some creature is his nearest relative is a conclusion to which we are driven by a consideration of the facts of zoological life. As regards prehistoric human remains

we do not find that the increasing resemblance to apes as we go back in time implies simian ancestry, seeing that these changes may be due to changes in food and posture, representing the acquisition of form growing out of function or closely correlated with function. In that case, man's increasing resemblance to apes has other explanation than descent from a common ancestor, being, if our interpretation is correct, a case of convergence, the response of similar form to similar function. As a matter of fact, the increase from long-headedness to short-headedness, which we find as we go from earliest man to more recent man of the prehistoric past, is a proceeding to greater resemblances with the apes. Round-headedness is a characteristic of apes no less than, in fact much more than, it is a characteristic of modern man. Here the resemblance is due to different factors working; in the case of round-headed man to the decrease in muscles and to upright stature; in the case of the apes the occiput is flattened to provide attachment for strong muscles reaching up from the neck region to support the head. Man's upright posture obviates the need for such marked occipital support, and the posterior projection of the occipital accounts largely for his greater length of head as compared with that of the apes. But this is only to say again that mere resemblances do not count for much; they must be interpreted in the light of the causes which give rise to them.

A word as to the bearing of these findings upon theories of evolution. If they look Lamarckian, that is only because the reader has not penetrated beneath the surface of the argument. This is not the place to discuss the relative merits of Darwinism, Weismannism or Lamarckianism, but if we understand their respective implications, there is nothing in our view which would not fit into any one of those schemes. The modification of form through function can proceed from generation to generation by the principles of Darwinian selection, if that is the evolution doctrine to which one is committed. It can

proceed, of course, with the mechanism represented by Weismann. Likewise, it is susceptible of Lamarckian interpretation if one be a Lamarckian.

But in any case we can not afford to blind ourselves to facts because we may shy from their implications. A good case is not strengthened by adducing poor reasons in support of it, and no fear of giving comfort to the enemy should lead us to suppose that a partial concealment of truth, which arises from concealment of part of the truth, can compensate for the value of unprejudiced consideration of the facts of life, whether they seem to fit into our larger scheme of evolution or fail to fit. No one can read the history of physical anthropology since the day of Darwin without seeing that the evolutionary idea has largely dominated its ambitions and determined its findings, sometimes, we are convinced, to the detriment of the truth. The duty of the anatomist, however, is not to plead a cause but to play judicial advocate, willing to hear and consider all evidence bearing on the case.

Our findings mean, possibly, nothing more than that the human and the simian type, respectively, have been relatively fixed for a much longer period than it has been our custom to regard them. We are constantly lengthening out the vistas of the past, and it may be that we must extend them beyond our present wont in order to find the point where human and simian forms have diverged into their present persistent types. Certainly one can no longer accept Java man as common ancestor, nor do any of the Tertiary remains of simia suggest common ancestry. If it be clear that present evidence is insufficient, that fact provides sufficient answer to the question of how we ought to interpret such evidence as we have. We must not convict the prisoner at the bar simply because we do not know who else committed the crime. The essential point is, Can we prove him guilty? And so with regard to a common ancestor.

TROPICAL CYCLONES AND THE DISPERSAL OF LIFE FROM ISLAND TO ISLAND IN THE PACIFIC

PROFESSOR STEPHEN SARGENT VISHER
INDIANA UNIVERSITY

EVIDENCE FOR AND AGAINST A PACIFIC CONTINENT

ONE of the mooted questions concerning the Pacific is how the biota now found upon the scattered islands got there. There are two great schools of thought in respect to the matter. One believes that the presence of numerous Asiatic forms can only be explained on the assumption that at some earlier time many of the now remote islands were connected into a continent. Some members of this school think that the continent extended as far as the Low Archipelago and Hawaii.¹ Others do not ask for so much land, but assume a southeastward extension of Asia, to include the East Indies, Philippines, New Caledonia, Fiji and Samoa. Certain large islands are also believed to have existed, for example, one that would include all the Hawaiian Islands and another that would unite the Cook, Austral, Society and Tuamotu islands.²

The other school of thought is opposed to the idea of a Pacific continent, or of vast islands in it, and to the extension of Asia and Australia beyond New Caledonia.³ They contend that the agencies distributing life from island to island are sufficiently efficient to have enabled the land

¹ Campbell, Douglass H., "Some botanical and environmental aspects of Hawaii," *Ecology*, Vol. I, pp. 257-269, 1920; Bryan, Wm. A., "Hawaiian fauna and flora," Proceedings First Pan-Pacific Scientific Conference, Vol. 1, p. 158, Honolulu, 1921; Scharff, R. F., "Distribution and Origin of Life in America," 1911.

² Pilsbry, H. A., "The dispersal and affinities of Polynesian land snails," Proceed. Pan-Pacific Scientific Conf., Vol. I, pp. 147-151, 1921.

³ Many geologists and biologists belong to this school, including T. C. Chamberlin, C. Schuchert, H. E. Gregory, D. S. Jordan, F. Muir, etc.

forms to spread to the remote islands upon which they are found.

However, there are several features of the distribution of land forms that are difficult to explain on the basis of prevailing winds and ocean currents. One is the fact that many of the forms of even the easternmost islands are related to Asiatic forms rather than to American forms. That is not true of all types of life; a considerable number of Hawaiian forms, for example, being derived from a few American ancestors. Many of the seed plants, birds and some insects were derived from Central American ancestors.⁴ But a large enough percentage of the forms are so Asiatic as to have led those scientists who have examined this particular type of evidence to doubt if the existing distribution can be explained on the basis of existing conditions. They have shown, for example, that a favorable wind (the prevailing trades) and current (the drift set in motion by the trades) should have given Hawaii many Californian and Mexican forms of littoral mollusca, if these agencies were effective in transporting these forms.⁵ Likewise, the believers in the theory of widespread lands and certain other workers point out that the prevailing winds and currents throughout the Pacific tropics are westward, and the numerous species of Asiatic descent must have advanced eastward against the prevailing winds and currents. Yet the wind and currents are the only important agencies, aside from man, that might have transported the plants and animals in question from island to island.

How HURRICANES CAN DISTRIBUTE LIFE

Is it not highly probable that tropical cyclones have played a part in the dispersal of life from island to island in the Pacific? Upon their equatorward side there are

⁴ Brown, F. B. H., "Origin of Hawaiian flora," *Proceedings First Pan-Pacific Scientific Conference*, Vol. 1, pp. 131-142, 1920 (seed plants); Muir, F., "Some problems in Hawaiian entomology" (insects), *ibid.*, and Henshaw, "Fauna Hawaiianensis," Volume Vertebrates (birds).

⁵ Muir, F., *loc. cit.*

often violent westerly winds, completely overcoming the prevailing easterlies. As pointed out in discussions of the courses followed, many storms move eastward, within the tropics, or just beyond the tropics.⁶ In moving eastward, the strong westerly wind on its equatorward side carries much with it, and sets up a strong drift as well. An illustration of the occasional power and persistence of this westerly wind is given by the renowned missionary John Williams, who, driven by cannibals from Hervey Island, drifted in an open boat five hundred miles to Tahiti with a constant westerly wind.⁷ Normally, easterlies prevail in that portion of the ocean.

The power of the wind to transport light objects through the air is frequently illustrated during hurricanes, as, for example, when land birds and insects are carried out to sea in large numbers. Indeed, the presence of butterflies and birds far out at sea has often been mentioned in connection with hurricanes. A specific case of interest is mentioned by Dr. F. Woods-Jones⁸ concerning insects at Cocos-Keeling Island in the Indian Ocean. During a severe northwesterly wind associated with a hurricane, hundreds of dragonflies were driven the seven hundred miles from Sumatra and Java, the nearest land, to this little island. However, as the island possessed no suitable environment for dragonflies the introduction was ineffectual in spite of the large numbers driven there. But if a marsh or other favorable environment for these insects should develop on the island, there is no question that within a short time some storm wind would stock it with dragonflies.

An actual increase of the permanent fauna of Cocos-Keeling Island took place during Dr. Woods-Jones' resi-

⁶ Visher, S. S., "Tropical cyclones of the Pacific with charts of tracks," *Monthly Weather Review*, Vol. 50, pp. 288-297, 583-589, 1922, and bulletin of Bishop Museum of Honolulu, 1924.

⁷ Williams, John, "Missionary Enterprises in the South Sea Islands," London, 1838.

⁸ Professor at Adelaide University, Australia. Remarks following my paper before the Royal Society of New South Wales, November, 1921.

dence there, shortly after they had added a new plant, tomatoes grown from seed. At the first the tomatoes had no enemies, but before the first crop was ripened, an insect pest was brought by the same cyclonic gale that brought the dragonflies from Java and Sumatra. Although Cocos-Keeling Island is in the belt of Trades, which blow with exceptional strength and persistence from Australia, almost no Australian species are found in the fauna. Dr. Woods-Jones believes this fact is an illustration of Alfred Russell Wallace's generalization that flying forms are rather well adjusted to the prevailing winds, just as aquatic forms living in a regular current commonly are adjusted to it so as not to be swept away. But the sudden, irregular, violent winds and currents sometimes associated with tropical cyclones take many individuals by surprise and carry them away from land.

Not only are animals with wings sometimes carried long distances by hurricane winds, but many forms attached to leaves are thus carried. The stripping off of almost all the leaves occasionally accomplished by hurricanes has been mentioned often. Some of these leaves are carried far, and on these parachutes are sometimes attached worms, larvae eggs or small snails.⁹

HURRICANE CURRENTS AS DISPERSING AGENCIES

The strength of the abnormal ocean currents set in motion by hurricane winds is mentioned repeatedly in the Pacific Islands Pilot.¹⁰ The significance of such abnormal currents may be illustrated by a statement concerning the Hawaiian Islands. A few years ago the mangrove was introduced upon the island of Molokai. In spite of strong normal currents at right angles to the favorable direction, seeds are occasionally floated to Oahu

⁹ Pilsbry, H. A., "The dispersal and affinities of Polynesian land snail faunas," Proceed. First Pan-Pacific Scientific Conference, Vol. 1, p. 149, Honolulu, 1921.

¹⁰ U. S. Hydrographic Office, Washington, 1920.

by abnormal currents, and the tree is now establishing itself there, more than twenty-five miles from Molokai.¹¹

The facts that most of the lowland plants and animals of the wide stretch from Fiji and the Carolines to the Low Archipelago and Hawaii are of the same or closely allied species, and that at the same time there is a progressive dropping out of species eastward, suggest strongly that the distribution of life forms has been from scattered island to island and has been accomplished by transporting agencies that are rather efficient, though not perfectly so. The fact that relatively few forms are of American origin (except remotely) suggests the inadequacy of the normal trade winds and normal currents as agencies of dispersal, in accord with Wallace's law concerning normal winds and currents. However, the relatively small part that South America has played in supplying forms to the Pacific Islands doubtless is due partly to two special conditions. One is found in the few islands in the eastern part of the tropical Pacific. Indeed, good atlases show no islands between the Low Archipelago and South America, about three thousand miles away. The Galapagos Islands, on the equator, are almost the only islands north of that zone in similar longitudes. South of 24° S latitude are only Easter Island (28° S), Sala Y Gomez (26½° S), and a few other islets or rocks to the west and northwest of Easter Island, and also San Felix and Juan Fernandez islands near the 80th meridian, not very far from South America.

The second special condition highly unfavorable to the spread of South American forms over the Pacific Islands is the fact that much of the western portion of tropical South America is almost barren of life, on account of the extreme aridity of the lowlands and the presence of the lofty Andes only a short distance from the coast. Some-

¹¹ Oral communication by C. S. Judd, territorial forester. Several illustrations of the significance of changes in ocean currents in the Atlantic are given in papers in the Proceedings of the First Pan-Pacific Scientific Conference, Vols. 1 and 2.

what similar conditions obtain over a wide belt in the North Pacific. There are almost no islands between Hawaii and North America, and most of the coast of Mexico is almost barren on account of aridity. On the other hand, the southeastern coast of Asia and the East Indies teems with forms adapted to the climatic and soil conditions which obtain in most of the Pacific Islands.

Another argument of advocates of great extensions of the lands is the following: they say that wind and currents, even those associated with hurricanes, apparently are not effective in the dispersal of certain types of life, as shown by the absence from the coast of Queensland of certain forms known in New Caledonia. Both the normal trades and numerous hurricanes pass over New Caledonia and thence to Queensland, and yet the coconut is established at only a few points on the Queensland coast, and certain species of land snails abundant in New Caledonia are unknown in Queensland.

The general lack of the coconut in Queensland appears not to be due, however, to a lack of seed there, for they are often noticed sprouting along the shore. The severe droughts during the cooler season of each year, characteristic of this part of Australia, may be the factor preventing their widespread establishment on this coast.

The absence from Queensland of the large showy land snail (*Placostylus*), common on the islands to the eastward, may be due to the presence in Australia of enemies that prevent their establishment. The Australian Bush-turkey feeds upon similar mollusca, and it has been suggested by Curator Charles Hedley, of the Australian Museum, as possibly responsible for the absence of this island snail in Queensland.

HURRICANE FLOODS AND LIFE DISPERSAL

Another way in which hurricanes have influenced the dispersal of land forms is in connection with the floods they cause, whenever excessive amounts of rain fall in a short time. There are numerous records of the fall of

more than ten inches in two days, and some records of more than sixty inches in three days.¹² Under such conditions normally rather small streams become rivers, and carry to sea vast quantities of driftwood. The river banks are eroded badly, and many trees are undercut and carried out to sea. During the excessive rains, large masses of dirt and loose rock upon steep hillsides often slip or slump, sometimes temporarily damming valleys. In case the dam breaks, the sudden rush of waters does its part to contribute natural rafts of driftwood, with their load of land animals and seeds. Furthermore, the animals are not nearly so likely to be picked off a raft by sea gulls or other birds during a hurricane as they are in ordinary weather. Hence, the absence of long rivers flowing into the Pacific, with the exception of the Chinese rivers, should not lead to the assumption that natural rafts of considerable size and biological dispersing possibilities are lacking in the Pacific.¹³

Tropical cyclones have also played a part in the distribution of peoples over the Pacific. Legendary accounts indicate that a number of island groups were discovered by occupants of boats that had been blown out of their course by storms. The discovery of New Zealand by Polynesians enroute from Samoa to the Cook Islands is a specific illustration.¹⁴

MAN AS AN AGENCY OF DISPERSAL

The great importance of man in distributing plants and animals of economic importance and, incidentally and in-

¹² Visher, S. S., "Tropical climates from an ecological viewpoint," *Ecology*, Vol. IV, pp. 1-10, 1923, and "Tropical cyclones of the Pacific," Bull. Bishop Museum, Honolulu, 1924.

¹³ Pilsbry, H. A., (*loc. cit.*) has made this erroneous assumption. He states: "The argument for distribution of animals by natural rafts has never been more convincingly stated than by W. D. Matthew in his paper 'Climate and evolution.' Much of his argument, however, is not applicable to the Pacific Islands. Here we have no large rivers to give forth natural rafts. If a single tree is washed to sea it must be very exceptional."

¹⁴ Best, Elston, "Polynesian navigators, their exploration and settlement of the Pacific," *Geographical Review*, Vol. 5, pp. 169-182, 1918.

advertently, of numerous smaller species concealed in the soil or bark or on leaves has been emphasized by several scientists.¹⁵

GEOLOGIC CHANGES

The dispersal of life from island to island over the Pacific has been accomplished slowly. Undoubtedly, during the geologic ages, there have been geologic changes that have been significant. For example, it is known that long ago there was more than once a strait where the continuous Central America now is. Conceivably at such times the drift induced by the Trade winds, and which is now diverted northward in the Atlantic to form the Gulf Stream, may have continued westward, carrying with it some of the seed plants and animals of the islands situated where Central America now is.¹⁶ Likewise, any tropical cyclones that occurred then in the Caribbean region would have been more likely than now to sweep westward far into the Pacific, for the atmospheric pressure conditions prevailing over the land, especially mountainous land, seem often to divert tropical cyclones.

Likewise, it is known that Australia was formerly connected with Asia by way of the East Indies and New Caledonia. At such times, it is probable that the normal ocean currents were distinctly different from the present. While now part of the equatorial current finds its way westward between the islands and enters the Indian Ocean, formerly the continuous land necessarily diverted the warm equatorial current into higher latitudes.

Another change during the geologic past, which is much more frequently mentioned, is the lowering of the sea level during the accumulation of the continental glaciers of the several ice ages. It is thought by some that the

¹⁵ For example, by Mayor, Alfred G., and Safford, W. E., in *Proceedings First Pan-Pacific Scientific Conference*, Vol. 1, pp. 15, 147, 183-187, and by Best, Elston, *loc. cit.* Safford has made especial study of the cultivated plants of Polynesia, *loc. cit.*, pp. 183-187. See also Guppy, H. B., "Observations of a Naturalist in the Pacific," Vol. 2, on "The distribution of plants and animals," London, 1908.

¹⁶ Brown, F. B. H., *loc. cit.*

sea level was lowered about sixty feet during the Pleistocene glacial epochs. Unquestionably there was some lowering of the sea level, but probably not nearly that much, for the glaciers probably were not nearly so thick as some have assumed.¹⁷ However, any considerable lowering of the sea would result in an increase in the land area, sometimes connecting neighboring islands, and hence facilitating the local spread of land forms.

DURATION OF GEOLOGIC TIME

The recent great increases in the estimates of the duration of the geologic past also has a bearing upon the subject of tropical cyclones and the dispersal of life in the Pacific. It is conceded that the chances of a single hurricane doing much along this line are small. The great reason why hurricanes have been largely ignored by the students of this problem is because hurricanes were believed to occur only at long intervals and were thought to be too rare to play much of a part. But now that it is known that more than a score occur annually, on the average, out in the Pacific (in addition to those in the Philippine region) they take on a different aspect. Their significance is also increased by the fuller appreciation of the diverse ways in which they affect the lands, streams and currents. They are also less likely to be ignored as a factor in the dispersal of life when it is realized that the interval since the beginning of the Mesozoic Era probably is many times the twenty million to fifty million years it was thought to be a few decades ago. Indeed, the remarkably convincing evidence, derived by leading physical chemists from the study of the products of the disintegration of radioactive substances in igneous rocks of various geologic ages, indicates that probably more than a billion years have elapsed since life became abundant upon the earth. Hence, fortuitous happenings, such as the dispersal of living forms by hurricanes, have had a long time in which to succeed.

¹⁷ Huntington and Visher, "Climatic Changes, their Nature and Causes," New Haven, p. 125, 1922.

SHORTER ARTICLES AND DISCUSSION

THE COMMENT ON SEX IN PIGEONS CONTAINED IN GEROULD'S PAPER ON BUTTERFLIES

IN a semi-detached position at the end of a paper recently published in *Genetics*¹—a paper dealing particularly with “white wing color in yellow butterflies”—Gerould² has discussed at some length two points involved in the work of Whitman and of Riddle on sex in pigeons. His discussion of the work on pigeons apparently has only a tenuous connection with his own study, but Gerould clearly gives his readers the following impressions: (a) That he has made and presented an “analysis” of the published data of Whitman and Riddle on sex-control; (b) that the statements made by myself concerning sex or sex-control rest merely or mainly upon the data which he claims to have reviewed; (c) that his “analysis” indicates that our data on this subject are without special significance.

Gerould presents so small a part of the two kinds of data which he assumes to analyze and in other respects is, quite unconsciously no doubt, so unfair, and the data involved are so little available to most readers of the journal which carries his article, that it seems necessary to call attention to some of the errors of his statement. Limitations of space, however, will permit neither the complete quotation of, nor special comment upon, all his remarks.

One should first consider the results obtained with butterflies which Gerould thought applicable to our results with pigeons—results which led to his meager examination of parts of the work of Whitman³ and of Riddle^(4, 5, 6). It would seem

¹ The management of *Genetics* was unable to publish a reply in that journal. In order that the readers of the original criticism may have the facts herein presented the author has been obliged to ask for publication elsewhere.

² Gerould, J. H., “Inheritance of white wing color, a sex-limited (sex-controlled) variation in yellow Pierid butterflies.” *Genetics*, 8: 495-551, Nov., 1923.

³ Whitman, C. O., Posthumous works; edited by Oscar Riddle. Vol. 2. Carnegie Inst. of Wash., Publ. No. 257, 1919.

⁴ Riddle, O., “The determination of sex and its experimental control,” *Bull. Amer. Acad. Med.*, 15: 265-284, 1914.

that the utter dissimilarity of reproductive conditions in these two groups might have suggested caution in making any comparisons whatever—particularly since, in the work of Whitman and myself, the sex-tendencies of ova were referred to highly specific conditions of reproduction in pigeons. But it appears that in the “paired eggs of pigeons” Gerould hoped to find a “precocity of male-producing eggs comparable to the normal condition in *Colias*.” He, and apparently all others interested, already knew (Gerould, p. 543), in the case of the earlier appearance of males from a brood (a large group) of eggs in *Colias*, “that these well-known facts are not due to an earlier laying of the male-producing eggs, but probably to a greater rapidity in the development of the male as compared with the female.” “Preeocity” of male-producing eggs in *Colias* therefore refers solely to a *more rapid development of the male than of the female embryos* of that group; and for any elucidation of this point one would suppose it necessary to look to *this same kind of fact* in pigeons. On this special and pertinent point was our published statement, in a paper which he does not cite⁵—possibly published too late for his inspection—that in pigeon embryos “we are unable to say, however, that a difference in ‘developmental rate’ is found for male and female” (p. 244). At no other time or place have we ever suggested that such a difference exists. *A priori*, one might have thought that more light would be shed upon the phenomenon of “more rapid embryonic development” of the male sex in *Colias* by comparing this with the “rate of embryonic development of the sexes” in pigeons, than by fixing the comparison on “the order of output of ovarian eggs” in pigeons!

It seems, moreover, that the appearance of a “predominance of males in the early season” from certain crosses of pigeons was also at first thought to be comparable, or in line with, the “precocity”—the more rapid embryonic development—of males from normal matings of *Colias*. The statement just made above obviously applies also to this doubly mismated comparison. It is remarkable only that such comparisons were attempted.

⁵ “Sex control and known correlations in pigeons,” AMER. NAT., 50: 385-410, 1916.

⁶ “Control of the sex ratio,” Jour. Washington Acad. Sci., 7: 319-356, 1917.

⁷ “On the cause of twinning and abnormal development in birds,” Amer. Jour. Anat., 32: 199-252, Sept., 1923.

These, then, were the mistaken considerations which led Gerould to some inquiry—in the work of Whitman and of Riddle,—concerning the “paired eggs of pigeons” (two eggs of clutch, the first—from most pure species—predominantly male-producing), and the predominant production of males in early season followed by predominant female-production later in the season (this from certain crosses, and after forced and crowded egg production). We may next consider the nature and completeness of his inquiry.

Gerould reproduces one particular table (summarizing the sex production records of three females of one particular cross) from the Whitman (3) studies (nothing was taken from either of the three papers cited from Riddle), and then says:

In the cross *T. orientalis* ♀ x (*St.*) *alba* ♂ an excess of males is said to occur in the spring months, whereas later in the season, *e.g.*, after July 1, females predominate. The offspring of three mothers are cited to establish this point. It is apparently on such meager data as these that Riddle's sweeping conclusions regarding sex control are drawn.

The actual facts could only have been stated in words similar to the following: That the offspring of these “three mothers” were specifically noted by the authors as *not* demonstrating, but as *bearing* on this point; that generic crosses generally, specific crosses also (72 types of crosses—listed on p. 10 of that study—practically all have a bearing), and much breeding without any crossing at all recorded in that volume, are all also cited as bearing on the matter; that in any and all cases *season* is not alone concerned, since several other modifying conditions were already named and described—and season itself is probably only indirectly involved through its relation to variable periods of fertility; that no attempt is made in the chapter cited, nor in other chapters of that volume, to present Riddle's studies on, or knowledge of, these several factors (for the reason that Whitman had recognized and considered only a few of them, and it was essentially his work that was being presented in the volume from which Gerould took one table); and that, in the same chapter from which this table was taken, it is plainly stated that all the data there considered “are perhaps not wholly conclusive. They do accord, however, with the results found generally in the other crosses, and a consideration of this matter may be undertaken in connection with these data” (p. 72).

But that the evidence for "sex control" in these or any other particular cases should be asserted to rest solely or mainly upon even all the "sex ratios" obtained is a further error which could not be made by any one who had read even the single chapter of the Whitman volume containing the table cited by Gerould. For example, in connection with this topic—seasonal predominance of the sexes—the following statement (p. 71) was there made:

The editor (*i.e.*, O. R.) is making extensive studies on many subjects connected with the size, chemistry and stored energy of the egg, and of the relation these bear to sex and fertility; on the relation of season and "crowding" of clutches to sex; and the question of the relative infertility of these hybrids. The results of these studies must appear later. The additional knowledge obtained from these sources, however, gives the editor confidence concerning some points of the present chapter which do not appear conclusive from the data available for the present volume.

Nor could this error be made by any one who had read and partially comprehended either of my own three short publications cited by our critic. One may therefore assume that Gerould had completely read none of the citations made to the studies of Whitman and of Riddle. In all my own three publications cited by Gerould there was plainly presented, by means of a figure or diagram, the *eight* (1914) or *ten* (1916, 1917) additional and distinct lines of study then being conducted, and which constitute my own *tests* of the reality of "sex control"; and all or several of these tests were also briefly described in the text of each of those three publications. Additional kinds of tests have been added and partially reported since 1919.

From the above it follows that in no sense is it true that "it is apparently on such meager data as these that Riddle's sweeping conclusions regarding sex control are drawn."

But Gerould further finds that the data of the single table actually examined are also unsatisfactory. In opposition it is stated: "The numbers are small and indicate a slight excess of male offspring." Surely the numbers (also the amounts and kinds of data examined!) are small. But what has the statement that the numbers "indicate a slight excess of male offspring" to do with the question? Is not the question whether these particular records do or do not show a predominance of males from the earlier season and a predominance of females later in the season? Could not the case be proved perfectly with

"a slight excess of male offspring"? Or, equally well with a slight excess of female offspring? Or, with exactly equal numbers of the sexes? This fallacy is again belabored within his paragraph when it is stated that

The small numbers of offspring (13 ♂♂, 16 ♀♀) of this mother (No. 54) indicate that the seasonal variation in the sex ratio is quite within the range of merely chance variation.

Despite the small numbers involved when single years are compared, and notwithstanding the amount of "lumping of data" which we warned was practised in such a summary, it can be seen by reference to the data for these individual birds (3; pp. 52, 53, 78, 79) that the sex ratio before and after July 1 is different in six cases (two cases showing equality include the *smallest* numbers of the series). In all these six cases the proportion of males is higher before July 1 than after. And, after separating the final period for one of these mothers—following November 29, 1914, and forming the actual beginning of a true early season period (as provisionally noted in table 44)—the total numbers obtained from the three mothers are 34 ♂♂ : 11 ♀♀ from the earlier period, and 26 ♂♂ : 32 ♀♀ from the later period. The two years (1906, 1909) of no "overwork" gave 5 ♂♂ : 1 ♀. Whoever wishes to do so may of course assure himself that these several figures are "quite within the range of merely chance variations."

Concerning the first of the two points discussed by Gerould it thus becomes clear (a) that his attempted comparisons between *Colias* and pigeons are unsound, (b) that he very inaccurately states the problem of periodicity in sex production and mentions no other factor than season as related to it, (c) that he ignores the fact that all the publications cited by him make it entirely clear that only a part of the data for any aspect of sex control has hitherto been published, (d) that he utilized only a part of the published data bearing on the specific question raised, (e) that he draws an unwarranted conclusion from the fraction of data which he examines.

Gerould next presents an "analysis" of a second point in the work of Whitman and of myself—the predominance, in some pure species, of males from first and of females from the second egg of the clutch. Here again we find: (a) He ignores completely—never once mentions—the point chiefly involved in a

discussion of this point (in so far as my own work is concerned), namely, the relation between yolk-size and sex; (b) he has totally failed to grasp or to intimate the fact that our studies on "sex control" manage to get on whether the eggs come in "normal order," "reversed order," or utter "disorder"; (c) he utilizes a part only of the only kind of evidence to which he refers; (d) he presents statements from other workers on hybrid forms (Cuenot, Cole) as though they are in contradiction instead of in complete confirmation of any words ever used by Whitman or myself on the subject; (e) he again refuses to draw the sane and necessary conclusion from the data actually cited.

A closer examination of all these several points can not be included here. Perhaps it will suffice to refer the reader particularly to pages 48, 72, 172, 173 of the Whitman (3) studies; to note that, in addition to the papers cited by Gerould, the writer has published twenty-two papers which deal with one or another aspect of the problem of sex control and sex production in pigeons; and to supply the accompanying tabulation of data on "sex predominance in the two eggs of clutch" contained in the particular publications which Gerould cites and presumably reviews.

The reader may next examine the summary table just mentioned. This table further indicates (by means of figures in parentheses) the part of these data actually found and utilized by our reviewer. Among hybrids only a single kind (one or another race of common pigeons) is cited by us here, though many kinds are available. Fragmentary data (or data having no relation to other problems) on common pigeons were not included in the Whitman publication; and, in the papers cited by Gerould, the present writer has published nothing whatever on this group. A few data for *C. livia* and *C. affinis* (wild) were not included here because breeding data have shown (3; p. 112) some of the individuals used were not pure but hybrid; none of my own data on these species is published. Individuals of *St. alba* whose purity was questioned for other reasons are also excluded. Otherwise, all data for all groups contained in the four publications cited by Gerould are included.⁸

⁸ The pages of the 1919 publication (3) on which the data may be found are as follows: No. 1; 34, 38, 39, 40, 51, 52. No. 2; 35, 38, 139, 140. No. 3; 117, 118. No. 4; 119, 120, 121. No. 5; 167, 168, 169. No. 6; 171. No. 7; 171. No. 8; 150, 153. No. 9; 81, 85, 96, 140, 145, 148, 151, 157, 164, 174, 175, 177 (Riddle, 1916: 392, 393). No. 10; 76, 77, 83, 84, 140, 145, 157, 163. No. 11; 148, 149. No. 12; 93, 104 to 110.

The table shows with sufficient clearness that only a part of the data in the studies cited was actually considered by our critic. But even the part considered he finds quite unsatisfactory. Why? He refers to six species. In every one of these six species the "sex pairs" did yield, in plain fact, more males from first eggs and more females from second eggs; and this is the sort of "predominance" of which we have repeatedly spoken—with the additional statement that "it seems probable that

TABLE 1

Data hitherto *published* (summarized here for first time) on order of males and females in pairs of eggs which produced the two sexes. Group 1: Pure wild species. Group 2: *Streptopelia* species, individuals of which are certainly sometimes contaminated with a related species. Group 3: Various races of common pigeons—all hybrids.

Group	No.	Kind of pigeon	Number of cases of:		
			Males from first egg and females from second egg of pair		The reverse
1	1	<i>Turtur orientalis</i>	23	(10) ⁹	9 (2) ⁹
	2	<i>Turtur turtur</i>	4		2
	3	<i>Zenaidura carolinensis</i>	5		2
	4	<i>Zenaida vinaceo-rufa</i>	5		0
	5	<i>Spilogelia suratensis</i>	5	(4)	3 (3)
	6	<i>Phaps chalcoptera</i>	4	(4)	0 (0)
	7	<i>Stigmatopelia senegalensis</i>	2 ¹⁰	(2) ¹⁰	0 (0)
	8	<i>Streptopelia humilis</i>	4		1
Total			—	—	—
Total			52	(20) ⁹	17 (5) ⁹
2	9	<i>Streptopelia risoria</i>	38	(21)	20 (8)
	10	" <i>alba</i>	13	(7)	6 (5)
	11	" <i>douraea</i>	1		2
	Total		52	(28) ⁹	28 (13) ⁹
Total			—	—	—
3	12	Common pigeons (homer; pouter; domestic rock).....	10		9

this order is normally reversed in some other wild species . . . and also in some individuals, etc." (3; p. 173). Again, the

⁹ Cases cited by Gerould completely given in these columns.

¹⁰ 12 ♂, 2 ♀ from first eggs; 2 ♂, 9 ♀ from second eggs (unpaired hatches).

small numbers of "unpaired" (sex known from one egg only) individuals cited do positively indicate the same thing. If, in disregard of this uniformity of the *six* groups, he was unwilling to conclude that the observed differences are significant the additional data available to him already prove his estimate a poor one. Such additional data were available for four of those six species, and in every case the earlier type of difference is clearly maintained when the additional or missing data are found and tabulated. Moreover, four additional (unmentioned by our reviewer) species of unquestioned purity all reinforce the evidence from the other six. All these ten species show—*despite the small numbers* obtained for most species—a predominance of males from first and a predominance of females from second eggs. All individuals of eight of these ten species were unquestionably pure, not hybrid. The total numbers for this group are, 52 to 17—a little better than a 3:1 ratio. Only one of the 11 species (*St. douraca*) represented in the table seems not to present a similar situation and here the numbers are the smallest of the series; in addition, the ancestry of the bird which produced the two reversed pairs (3; p. 148) was not recorded and may not have been pure *douraca*. Further, we have stated no "rule" for *all* pure species. For the three species of this second group, which almost certainly includes some *individuals* which were not pure, the numbers obtained are 52 to 28. Finally, the only hybrids listed (homer, pouter, etc.) show essential equivalence, 10 to 9.

Perhaps these paragraphs will assist the reader to a truer estimate of the nature and extent of Gerould's "analysis," and of the soundness of the conclusions which he draws from it.

In conclusion, I trust it is wholly true that I have made some "extensive conclusions regarding sex control." I am now finding occasion further to extend some of them (and to qualify a few). Any statements made, however, have been made upon the basis not only of all my own data—published and unpublished—and of those of Whitman, but upon all other relevant data known to me as well. Fortunately, the present attainment of analogous sex studies in the hands of others is such that the essential points in physiological sex theory urged by Whitman and by myself would now be largely established even if our work be left quite out of account. That advance is now well under way—so well,

that one may even now recall the exhilaration of falling into step when the line was thin and the goal in doubt.

OSCAR RIDDLE

CARNEGIE STATION FOR EXPERIMENTAL EVOLUTION,
COLD SPRING HARBOR, L. I., N. Y.

THE EFFECT OF X-RAYS ON THE FERTILITY OF RATS

THIS paper is a preliminary report of some work on the effects of X-rays on rats, conducted in the genetics laboratory of the Bussey Institution. The X-raying itself was done at the Jefferson Physical Laboratory, and acknowledgment is due to Professor William Duane and Dr. G. L. Clark for generous assistance in devising apparatus and help in using it.

METHODS

Only males have been rayed, and only the region of the testes themselves has received the rays. To accomplish this, a wooden box was completely sheathed with sheet lead 2 mm in thickness. To the inner side of the sliding door of the box the rat to be rayed was fastened. When the door is slid into position, the serotum of the rat comes exactly opposite an oval opening in the lead sheathing. Thus the whole body of the rat, except the region of the serotum and the parts immediately overlying it, will be protected from the rays, the object being to ray the germ-cells and as little besides as is possible. See Figures 1 and 2.

In order to be positive that rays entered the box, a photographic plate was wrapped in black paper, and placed in the box in the same position as the rat would be placed. It was exposed for three seconds. The result was that the plate was blackened strongly and uniformly over the area opposite the opening in the lead sheathing, but nowhere else.

The rats were etherized, to keep them quiet, strapped to the door, and exposed to the X-rays for varying lengths of time. On dosages of more than 20 minutes, the rat was rayed in twenty-minute stretches, to insure his remaining quiet and in position throughout the treatment, with 20 minutes between successive exposures. A convenient voltage and amperage were arbitrarily selected, as follows: 65,000 volts, 3 miliamperes. The rats were placed at a distance of 40 cm from the edge of the bulb. A tung-

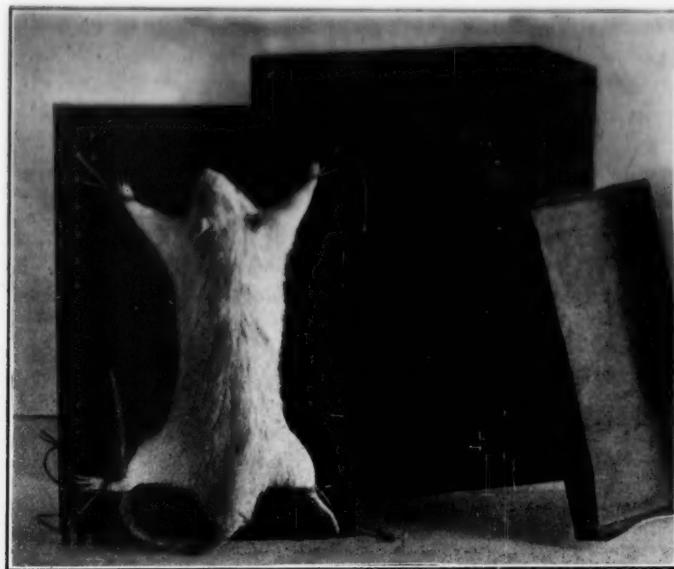


FIG. 1. X-ray box, front view, showing oval opening in lead sheathing and rat strapped to sliding door. Lead cover for the box is shown at right.

sten X-ray tube was used. These relations were kept constant throughout the experiments, but the time of exposure was varied.

At first a thick aluminum filter was used: later a thinner one. Then, as no "burning" effects were found, the filter was discontinued.

The experiment was started by exposing rats for periods varying by five-minute steps from one minute to an hour. Each X-rayed male in this experiment was tested for fertility by keeping it constantly associated with fertile females, alternating it every three weeks between two cages of females, so as to further insure a valid test of its fertility.

RESULTS

It was found that all rats rayed up to an hour, using the thick filter, remained perfectly fertile, regularly producing normal, healthy litters. Then a thin filter was used. Rats rayed up to 35 minutes were normally fertile, but those rayed for 40 minutes

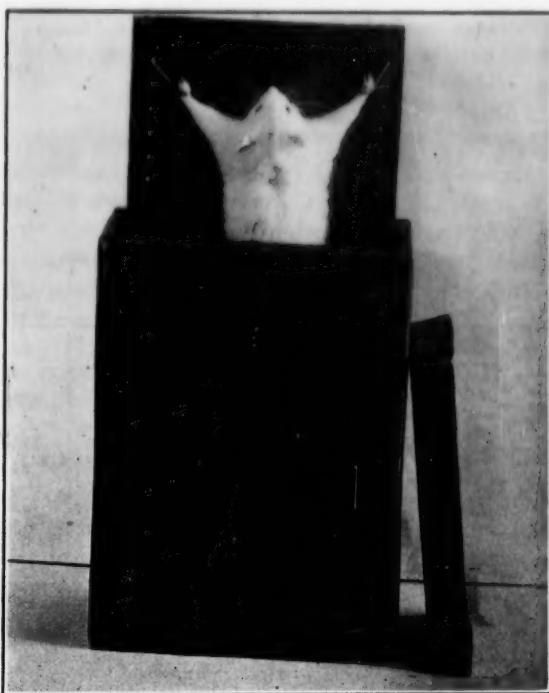


FIG. 2. X-ray box, back view, showing rat being placed in position.

went through a sterility period, to be described farther on. When this result was found, the filter was discarded altogether; and rats rayed without the filter behaved just as rats rayed with the thin filter, that is, exposure up to 35 minutes did not effect fertility, while a 40 minute exposure caused the sterility period. It should be noted, however, that with the thick filter no sterility followed, which indicates that the soft rays, of long wavelength, are the effective rays.

The rats which were rayed for 40 minutes with a thin filter or with no filter, behaved as follows. For the first few weeks they were normally fertile, litters being produced as long as 66 days after raying. After this fertility period, which varied in duration among the individual rats, a sterility period, quite marked, appeared, during which absolutely no young were produced.

After two months or more of sterility, fertility again appeared in full force, large healthy litters being produced regularly. Table I shows the details of the sterility periods to date.

TABLE 1

Rat No.	Litters produced after x-raying and before sterility.	Average young per litter.	Time from x-raying until last litter produced before sterility.	Time from x-raying until first litter produced after sterility.	Sterile interval.
10	6	6	55 days	120 days	65 days
66	6	5	66 days	110 days	44 days
167	3	6	62 days	146 days	84 days
182	*	*	*	136 days	*
185	1	5	24 days	156 days	132 days
215	3	6	65 days	119 days	54 days
227	2	8	27 days	150 days	123 days
231	3	5	49 days	141 days	92 days
average			49.7 days	136 days	85 days

The litters produced before sterility are presumably produced from sperm mature at the time of X-raying. If this is so, we may have a clew to the length of time mature sperm can live in the testis and epididymis. The first litter produced after sterility may well be considered the critical litter, as it is produced from germ-cells which must have just escaped being killed. These might conceivably be affected in some way. Therefore the first litter produced after sterility in each case is being kept and carefully studied.

To date, eight litters have been recorded, each of which is the first litter produced by some male after his sterility period. From some of these, F_2 young have been raised, all of which appear normal. These are being back-crossed to their parents, as a means of detecting any recessive genetic changes which may have occurred.

Although as yet no genetic changes due to the X-rays have been detected, the fact is thought to be of interest that a differential resistance apparently exists between spermatozoa and some early stage of the germ-cells on one hand, and the intervening develop-

* Kept from females until 75th day.

mental stages on the other, the latter obviously being much more sensitive to treatment. An effort will be made to determine the sensitive stages more precisely.

POSTSCRIPT

Not until this paper was ready for press did I discover a preliminary report by D. R. Hooker, in the *American Journal of Hygiene*, II, Proc. 461-2, on the effects of X-rays upon rats. Apparently, however, Hooker's approach to the problem is from a medical standpoint rather than a purely genetical standpoint, and I do not think that my work involves any unnecessary repetition of Hooker's experiments.

LAURENCE H. SNYDER

STATE COLLEGE,
RALEIGH, N. C.

EVIDENCE OF STRUCTURE IN THE GENE

In the last few years the amount and variety of data concerning gene variation have reached a point where it should be possible to make a general explanation that will at least serve as a working hypothesis. An explanation of gene mutation is suggested by some recent results from the highly mutable allelomorphs of the bar series in *Drosophila*. These results indicate that the gene consists of a main particle, or base, firmly fixed in the chromosome, with varying numbers of other particles, or modifiers, attached to it. The modifiers of any gene are usually attached to the base in a side-chain arrangement. Mutation consists of the gain or loss of modifiers or chains of modifiers.

(1) Two cases of coincidence of mutation occurred where one full-eyed mutant and one ultrabar-eyed mutant were found among the offspring of a single bar female. The female is emphasized since other evidence indicates that almost all the mutations of the bar gene occur in the female. The male in one case was bar-eyed and in the other full-eyed. The probability that these mutants were due to independent causes is of the order of one chance in a million. Bar eye is intermediate between full eye and ultrabar eye. In these cases both extremes arose simultaneously and it seems that one of the two bar genes in a germ cell of the female had lost something and that the other gene had gained something.

(2) The facet count of homozygous bar females is strikingly similar to that of full-ultrabar heterozygotes in those cases where the three allelomorphs of the series are derived by mutation from one stock and hence have the same titre of accessory factors. One dose of ultrabar is as effective as two doses of bar in reducing the facet number of the full eye. The difference between the full gene and the bar gene is the same as the difference between the bar gene and the ultrabar gene.

(3) The evidence indicates that one of the two bar genes of a female germ cell had lost something and that the other bar gene had gained by exactly that same amount. On the general thesis that losses can occur more readily than gains, the relative rates of mutation in the two directions should show which had lost and which had gained. Zeleny's data show that bar mutates to full about twenty times as often as it mutates to ultrabar. Therefore, the full gene is a bar gene minus something and the ultrabar gene is a bar gene plus something.

(4) This something which the bar gene may gain or lose is the *modifier* and the part to which it attaches is the *base*.

Bar mutates to ultrabar about three times in a hundred thousand flies, presumably due to the addition of a modifier subtracted from the homologous gene in a female. The full gene, however, does not add a modifier to form a bar gene so readily. Among all the millions of fruit flies so carefully examined, only one bar mutant has been found. This indicates a different order of mutation. It seems most probable that the full gene consists of a base alone and that the bar mutant arose by the addition of a modifier from some other locus.

(5) The ultrabar gene with its two modifiers mutates to full with about the same frequency as the bar gene with its one modifier. This would not be expected if both the modifiers of the ultrabar gene were attached to the base, since two breaks would have to be made as against one in the bar gene in order to attain the full condition. Therefore, it seems that the second modifier of the ultrabar gene is attached to the first modifier and not to the base. Furthermore, ultrabar mutates to full almost twice as often as it mutates to bar. This is to be expected, since pressure applied to the chain of modifiers would cause the greater strain next to the base.

(6) Sturtevant and Morgan have demonstrated that bar to full mutation is accompanied by crossing-over in that region of

the chromosome. Crossing-over is generally thought to involve intimate contact at the point of breaking. The mechanical dislocation of the modifier of the bar gene due to this intimate contact can readily be visualized.

(7) Since the facet counts of full, bar and ultrabar males resemble the facet counts of the corresponding homozygous females more than any of the heterozygotes, it is evident that the ratio of the number of modifiers to the number of bases is the potent factor determining facet number. The rate of change of facet number caused by successive additions of modifiers to the bases should give some indication of the facet number of possible allelomorphs with more modifiers than ultrabar. Excluding full since it has no modifiers, and taking the average of the counts for the bar female and the full-ultrabar heterozygote, since they have the same modifier-base ratio; the four following numbers remain in Zeleny's series: 400, 35.8, 25.7 and 22.0. The successive additions of modifiers not only cause a decrease in facet number, but the rate of decrease and the rate of the rate of decrease also become smaller. This indicates that all further additions of modifiers will give a facet count very slightly smaller than ultrabar. In effect, these allelomorphs with four or more modifiers would be completely dominant over full.

(8) A number of other measured character changes caused by mutation at the bar locus agree with the facet number data in that bar is intermediate between full and ultrabar, and that the bar female is similar to the full-ultrabar female.

(9) This explanation of the phenomena of mutation in the bar series also applies to those cases in other animals and plants in which considerable data have been accumulated. In some of these series of allelomorphs, however, there are members that can not be construed as quantitative variations of one kind of modifier, and occasionally these qualitatively different members also show a marked change in the rate of mutation. In such cases it seems that more than one kind of modifier is acting.

(10) An inspection of the chromosome maps of *Drosophila* shows that the loci of the various mutants are not distributed at random throughout the length of the chromosome, but are concentrated into certain regions. A comparison of these maps with the cytological figures shows that in almost every case these highly mutable regions correspond with the points of spindle fiber attachment. If these maps give a true picture of distance,

it is difficult to see why this relationship should exist unless mutation involves a mechanical alteration of the gene.

A later paper will discuss the general application of this hypothesis more fully.

DAVID H. THOMPSON

UNIVERSITY OF ILLINOIS

ON THE OCCURRENCE OF THE LARVAL STAGES OF
SCYPHOZOA IN THE ELKHORN SLOUGH,
MONTEREY BAY, CALIFORNIA

To the writer's knowledge, the literature of scyphozoan development is conspicuously lacking in any account of the abundance and conditions of occurrence of the larval stages in nature. It appears that the accounts of the development of *Aurelia* are all based upon stages reared from eggs in the laboratory, or upon material procured from collectors at Naples. The only statements bearing upon the present data are the following, in Sumner, Osburn and Cole's "Biological Survey of the Waters of Woods Hole and Vicinity":¹

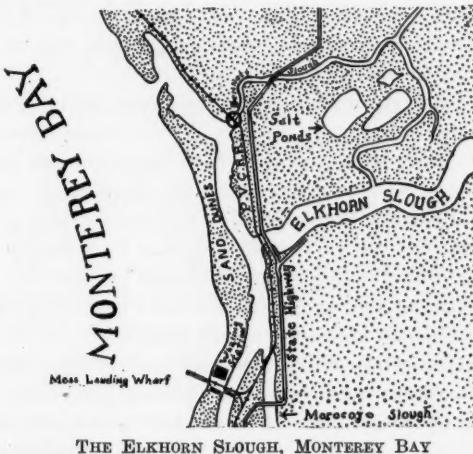
Young stages recorded by several observers as early as March; adults as late as September. Dr. Hargitt thinks it likely that sexual reproduction occurs in summer, the resulting scyphistoma larvae remaining in that condition till the following spring, when ephyrae are produced.

This paper, however, notes nothing further, either as to the abundance of the larvae or as to their habitat. Mr. G. M. Gray, of Woods Hole, in reply to an inquiry regarding these points, was unable to give the writer any definite information. Since any abundance at all comparable with that to be reported here could not have failed to impress the workers referred to above, it is believed that the present record may be of particular interest.

The accompanying map will suffice to show that the Elkhorn Slough constitutes the greater part of a considerable system of tidal estuaries emptying into the central part of Monterey Bay. The region of particular interest for this report (enclosed within a circle on the map) lies a few yards up the channel of a small branch (Bennett Slough) which joins the main channel at a point about one half mile below its mouth. This region may be conveniently located by the fact that it underlies a small trestle, over which the Pajaro Valley-Consolidated Railway crosses Bennett Slough. On extreme low tides, the water nowhere in this region exceeds three feet in depth, and is considerably shallower

¹ Bull. Bureau of Fisheries, XXXI, 1911.

over the greater part of the area in question. Here, along the sides of the channel, and over its bottom, a stratum of rather large rocks has been superimposed upon the sand and mud, presumably having been put there to support the railroad embankment.



THE ELKHORN SLOUGH, MONTEREY BAY

In the early part of November, 1922, the writer discovered vast numbers of scyphistomae on the under sides of rocks in three small, localized parts of this region: (1) Well toward the bottom, a few yards below the bridge, on the south side of the channel. (2) in the middle of the channel, a few yards below the bridge, and (3) in very shallow water (1 foot at low tide), in the middle of the channel, a few yards above the bridge. In these spots the scyphistomae occurred in such dense profusion as to form numerous white patches, some of over a square foot in area, on the rocks. Their distribution is sharply limited to the above described regions; careful search for them on the piles and cement walls of the trestle, and of a near-by bed of eel-grass, having been absolutely fruitless.

Since the date of discovery, this association has been carefully observed at intervals covering approximately sixteen months. In all, thirteen trips were made to the locality. The results of these observations may be summarized as follows:

(1) Only scyphistomae were found in November and December, 1922.

(2) In February, 1923, most of the larvae had formed large, well-developed strobilae, and were actively giving off ephyruleae. The strobilae are of a light, brownish color.

(3) In April, 1923, many strobilae were still present. Many were quite small, and the general color was rather lighter than noted in February.

(4) On October 9, 1923, the same situation obtained as in November, 1922; only scyphistomae were found.

(5) Strobilae were not again found until March 14, 1924, although observations were made later in October, and in December, 1923, and on January 9 and 31, 1924.

(6) On each trip mentioned, larvae were found in the locations described in a former paragraph, but never elsewhere.

Unfortunately, it has, as yet, been impossible to determine definitely the species to which these larvae belong. All three stages seem to agree perfectly with the descriptions given for *Aurelia aurita*. However, it is possible that they may be the larvae of a species of *Pelagia*, or of *Chrysaora gilberti*, since adults of these species, as well as of *Aurelia*, have been observed drifting through the channel in the strong tidal currents. No analysis of the water of the region has been undertaken, though the nature of its fauna, consisting of numerous Hydroids, Chitons, Nudibranchs and Serpulae, and occasional starfish and actinians, would indicate a salinity not greatly different from that of the bay.

The presence of great numbers of larvae at all seasons recorded, and their absolute restriction to three very small areas would indicate to the writer that the aggregations of larvae persist for several years, under favorable conditions, and that after periods of strobilation occurring in later winter or early spring, the larvae remain quiescent as scyphistomae over the summer and fall months, again resuming the production of ephyruiae late in the next winter. At present it is, of course, impossible to make any statements as to the number of times this cycle may be repeated, or of the factors calling forth its various phases. However, if we suppose the foregoing account to be a correct one, this unique sequence of events may constitute favorable material for physiological investigations of the life history in general.

Both the extreme abundance of larvae in the region considered in this report and the evidence of the long span of their active life are suggestive of the type of resources which may account for the hordes of jellyfish which appear annually along our shores.

A. E. GALIGHER

PACIFIC GROVE, CALIFORNIA

